RESPONSE OF NEW ZEALAND BIRDS TO THE PRESENCE OF NOVEL PREDATORS

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

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UNIVERSITY OF CANTERBURY

BY ROBYN WHITE

University of Canterbury

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ABSTRACT

Predation is the highest cause of mortality for birds and can place intense selection pressures on their behavioural traits. A number of studies have shown that some animals have innate predator recognition, while others which are predator-naïve have been unable to adapt to the introduction of exotic predators. For my thesis, I firstly studied how eight species of introduced and native birds respond to model predators at their nests. This enabled me to determine whether the native birds have been able to adapt to introduced mammalian predators and have developed recognition of them being a threat. In most species, the reaction to the stoat (*Mustela erminea*) (an introduced predator) was similar to that of a model morepork (*Ninox novaeseelandiae*) (a native predator). This suggests these species can successfully recognise introduced mammals as a risk. It also allowed me to test whether recently introduced birds have any innate recognition of snakes, which are a significant nest predator in their native ranges but do not exist in New Zealand. I found that introduced birds did not appear to have any recognition of snakes as being a threat. These losses and gains of recognition may have been caused by evolutionary changes or they may be influenced by learning and experience.

Secondly, I examined how South Island robins (*Petroica australis*) on a predator-free island responded to predator models and compared this to the responses of robins on the mainland (where they co-occur with mammalian predators). The island birds were assumed to show the ancestral reactions to mammalian predators, while any differences in response shown by the mainland robins would indicate they had acquired these behaviours in response to increased predation risk. I found that the island robins did not appear to recognise or react to a taxidermic mount of a stoat while mainland robins did respond to the stoat, confirming that at least some native birds can develop recognition of novel predators.

Finally, I compared the personalities of South Island robins on a predator-free island and on the mainland (where mammalian predators are present). I tested where individuals placed on the 'bold-shy' continuum by observing their willingness and speed to approach a risky situation in order to collect food. Studies have shown that average personality between populations can differ where predation risk differs. I found that the island robins were on average bolder than mainland robins. They came nearer to the observer and were faster to approach and remove a food item, while mainland robins were less likely to approach, and those that did approach took a longer time. It is likely that these differences were due to selection pressures by mammalian predators favouring shy individuals on the mainland while other pressures such as interspecific competition favours bold individuals on the island. Personality has been shown to be genetic and heritable, however, learning and experience cannot be ruled out and may also play a part in influencing how personality is expressed.

Together, my results support the importance of historical and ontogenetic factors in influencing how predator recognition and personality traits are expressed.

CHAPTER ONE: GENERAL INTRODUCTION

PREDATOR RECOGNITION

Nest predation is a leading cause of mortality in birds (Ricklefs 1969; Martin 1995; Colombelli-Negrel, Robertson & Kleindorfer 2010). There is strong evolutionary pressure on birds to minimise nest predation, which has lead to a variety of defence strategies. Nest defence has been defined as "Behaviour that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent (Montgomerie & Weatherhead 1988)". Nest defence strategies include active defences such as alarm calling and aggressiveness, passive defences such as nest location and crypsis, and social defences such as mobbing and colonial or protective nesting (Lima 2009).

Alarm calls are vocalisations which are expressed when danger is imminent (Hollen & Radford 2009). The function of alarm calls is still largely unresolved. They may be used for confusing the predator, warning the offspring or mate, or to attract other birds to mob (Serra & Fernandez 2011). Alarm calls have costs as they may attract the attention of the predator to the calling) bird. Thus, some authors suggest that alarm calls may be altruistic (Hollen & Radford 2009). There is some evidence that shows offspring react to parental alarm calls in ways that should reduce predation risk. Begging by chicks is typically conspicuous in order to attract the attention of the parents but it may also attract predators (Briskie, Martin & Martin 1999). Thus, there is an incentive for offspring to cease begging when predators are within hearing distance. For example, Southern house wren (*Troglodytes musculus*) chicks were quieter and stiller when parents alarm called (Serra & Fernandez 2011). The alarm calls made by wrens have also been shown to vary with different predators, suggesting that they

are passing information about the predator identity to a receiver (Fasanella & Fernandez 2009). However, it is has also been suggested that chick response in some species may have arisen through eavesdropping on signals intended for a mate or neighbours rather than being the main reason for the parents call (Serra & Fernandez 2011).

To actively defend their nest, birds may physically attack a predator, while swooping back and forth, dive bombing and alarm calling. This is thought to be an even riskier behaviour to the parent than just alarm calling as it may result in injury or death from the predator. However, if successful, attacks can force the predator to leave the area and it may be deterred from re-visiting (Grim 2008). The costs of directly attacking a predator could be lessened by recruiting other individuals to attack at the same time, a behaviour call mobbing. Mobbing can include interspecific neighbours as well as conspecifics, which together harass a predator, moving back and forth, occasionally touching or attacking it (Grim 2008; Krama et al. 2012). Mobbing may confuse the predator, advertise to the predator that it has been spotted or attract the predator's predators (Olson et al. 2013). However, there is also a risk to mobbing birds. For example, other predators may eavesdrop and be attracted to the commotion (Krama & Krams 2005). Pied flycatcher (*Ficedula hypoleuca*) nestboxes subjected to playbacks of recorded mobbings suffered higher predation, as martens (*Martes martes*) were alerted to the nest's location (Krama & Krams 2005). Because of the potential costs, mobbing may be a form of reciprocal altruism (Krams et al. 2010) as a bird aiding in defence of another's nest obtains no immediate benefit. However, the future benefits of reciprocal mobbing make it worthwhile, especially if cheaters receive reduced or no future aid in mobbing as shown in red-winged blackbirds (*Agelaius phoeniceus*) (Olendorf, Getty & Scribner 2004). It is also suggested that birds benefit from mobbing as they can learn and gain information on predators, such as their appearance and abundance in their territories (Curio, Ernst & Vieth 1978; Grim 2008; Berzins et al. 2010).

Whatever the level of response elicited in nest defence, the first step however, is the ability to successfully recognise a predator as a threat. To defend a nest, birds must first be able to accurately identify threats. The misidentification of (or inability to identify) a potential intruder near the nest may result in either a nest being depredated (as the nest owner does not respond appropriately to the threat) or energy and time being wasted by responding to something which is not a threat. Thus, there should be strong selection pressure to be able to recognise and react appropriately towards nest predators because the costs of failure to do so are high. However, nest defence behaviours are often costly and thus there are likely to be tradeoffs with other activities such as foraging (Brown 1999; Verdolin 2006). If a species becomes isolated from a predator for long time during its evolution, then it may lose the ability to recognise and respond to that predator as it pays the cost of maintaining recognition and nest defence behaviours without any benefit. Whether predator recognition persists may depend on whether recognition is experience dependent or hard wired and innate. (Blumstein 2006).

Unlike birds in continental areas, endemic New Zealand birds have been geographically isolated from mammalian predators for most of their evolutionary history. It has been at least 82 million years since there was a land connection with Australia (Cooper & Millener 1993), although most of the avifauna has colonised New Zealand and speciated more recently. Nevertheless, birds in New Zealand were still subject to predation over the course of their evolution, but these predators were other birds such as owls and raptors and not mammals. This key difference in predatory guilds is likely to have led to the evolution of quite different nest defence responses. As endemic New Zealand birds experienced predation from avian predators, selection should have favoured their ability to recognise and respond to this guild of predators. In contrast, innate recognition of mammals may have been lost or become inappropriate. For example, many native New Zealand birds respond to the presence of an

avian predator by sitting still on their nest. This may be effective for dealing with avian predators which rely on visual and acoustic cues to detect prey, but may not be effective against mammalian predators, which use their olfactory senses to a greater extent (Sih et al. 2010).

However, animals are not necessarily evolutionarily trapped and can adapt to new threats. The ability to adapt to a novel predator may depend on whether the animal has been ontogenetically isolated or evolutionarily isolated. If ontogenetic isolation has occurred, it may only take experience and learning for an individual to recognise to a predator (Griffin, Blumstein & Evans 2000). On the other hand, evolutionary isolation may mean that anti-predator responses have been lost from a species' genes. Reacquisition may depend on the species having experience of other similar predator guilds, or if it carries a general anti-predator response that using this against the novel predator provides a net benefit (Blumstein 2006). Selection pressures can favour individuals that do react appropriately (Réale & Festa-Bianchet 2003), or they may learn via social communication or through experience (Curio et al. 1978), resulting in successful predator recognition.

PERSONALITY

Recently, views about behavioural responses have changed from that focused on stabilising selection typically favouring an optimal response (and thus typical in a population), to that of alternative responses maintained by selection. Individuals in a population can exhibit consistent intraspecific variation in behaviour, which is commonly referred to as personality (Sih, Bell & Johnson 2004; Reale et al. 2007). A number of species have been shown to exhibit consistent personality traits (Gosling & John 1999). Based on such studies, Reale et al. (2007) suggested five categories of personality: (1) shyness-boldness, defined as an individual's reaction to a risky but not novel situation, (2) exploration-avoidance, defined as a

reaction to a novel situation (which can also be risky), (3) activity, defined as the general level of activity, (4) aggressiveness, defined as antagonistic reactions towards conspecifics, and (5) sociability, defined as the reaction to presence/absence of conspecifics. Each category should be considered as a continuum rather than bimodal, though individuals can exist at the extreme ends as tendencies. Individuals should also be relatively consistent in their place on the continuum for each category, though this may change with environmental conditions, season and age or life stage (Reale et al. 2007).

An animal's personality can be expressed in many different ecological contexts, such as in foraging (Bergvall et al. 2011), nest defence (Burtka & Grindstaff 2013), aggression (Bell & Sih 2007) and tameness (Barnett et al. 2013). Although personality is often considered on an individual level, it can also be applied to different scales, such as when comparing two populations (Reale et al. 2007). Multiple personality tendencies may be able persist in a population due to tradeoffs. However, if conditions change or differ, directional selection can favour one personality tendency, causing it to become more prevalent over time.

Predation has been shown to have selection pressures on a population's average personality (Bell & Sih 2007; Hollander et al. 2008; Bergvall et al. 2011; Dosmann & Mateo 2014). Different populations of the same species can therefore have varying average personalities as different traits are more or less successful under differing predation regimes (Brodin et al. 2012; Dingemanse et al. 2012; Miranda et al. 2013). For example, common frog tadpoles (*Rana temporaria*) from a predator-free island were bolder and faster at exploring a novel environment than conspecifics from a mainland population (which experienced greater predation risk) (Brodin et al. 2012). There has been speculation that experience and exposure to predators may be what generates personality, such as shown in three-spined sticklebacks (*Gasterosteus aculeatus*) exposed to trout (*Oncorrynchus mykiss*). (Bell & Sih 2007). There is potential for plasticity and variability among individuals which may change to some extent

with life stage (Herde & Eccard 2013). However, many studies have found that personality is heritable and consistent across environmental variation (Miranda et al. 2013; Brent et al. 2014; Dosmann & Mateo 2014). It is therefore likely that genetics form the basis for personality, but ontogenetic factors may play a role in shaping an individual's trait expression.

CONSERVATION

Predator recognition has important conservation implications for New Zealand birds. The introduction of exotic predators has devastated many island avifaunas (Steadman 1989) (Blackburn et al. 2004). For example, the introduction of mammalian predators has been implicated in the extinction of over 40% of all New Zealand birds (Holdaway 1989). Thus, it is important to understand why island birds are vulnerable to introduced mammalian predators and whether future introductions of other novel predators might place them at even greater risk. New Zealand provides a perfect setting to investigate how previously naïve populations of island birds respond to novel predators and how their response varies with experience as populations of some species co-occur with novel predators while others (primarily on offshore islands) have never been exposed. Previous studies have shown that some native bird species have gained or lost anti-predator behaviours within short time frames (Massaro et al. 2008; Jamieson & Ludwig 2012), suggesting that the ability to recognise novel threats is not fixed and populations may adapt to new predatory regimes.

In order to restore New Zealand's endangered bird populations, translocation programmes, in which birds on predator-free islands are transferred to mainland areas, are commonly used (Seddon, Armstrong & Maloney 2007). If anti-predator behaviours have been lost or diminished on such islands, reintroductions may not be successful unless predators are heavily controlled. One of the predictors of how successful translocations are is the presence

of predators (Snyder et al. 1996). Some species do have a certain degree of plasticity in their behaviours and have shown to be able to adapt to changes in predation risk though this may depend on the level of endemism (Duncan & Blackburn 2004) or time of geographic isolation from mammalian predators (Blumstein 2006) or physiological traits (*i.e.*, retaining ability to fly). There has been suggestion that predator-training naïve individuals can improve survival after translocation (Griffin et al. 2000) although it is unknown if training will last long periods or across generations. Even so, without control and eradication of mammalian pests, bird species in New Zealand continue to decline, showing that predator management is an essential part of restoring New Zealand's fauna and flora (Innes et al. 2010).

New Zealand birds are also at risk of future introductions of exotic predators. Snakes are a group of novel predators which do not occur in New Zealand, but which are at risk of future accidental establishment through increased trade. The introduction of snakes to previously snake-free Guam lead to the extinction or decline of many bird species on this island (Savidge 1987; Fritts & Rodda 1998) and thus a similar event would likely pose a serious risk to the birds of New Zealand. It has also been suggested that each additional exotic predator has a cumulative effect on native island species, as functional diversity increases and predators facilitate each other (Blackburn et al. 2005). Likewise, birds on predator-free islands are also at risk as mammals have the potential to accidentally arrive and colonise.

OUTLINE OF THESIS

The overall objective of my thesis was to examine how New Zealand birds respond to novel predators. For this purpose I examined three groupings of birds: a relatively naive species without any recent exposure to mammalian predators; native species that have only had *c.* 700 years of sympatry with kiore (*Rattus exulans*) and *c.* 130 years of other mammalian predators (King 1984; Worthy & Holdaway 2002); and introduced species which have

coevolved with mammalian predators (and continue to be sympatric with many of these predators in their introduced range), but are no longer sympatric with snakes, a significant predator in their native ranges (Weatherhead & Blouin-Demers 2004). I also looked at how personality might differ between the first two groups and how the difference in predation risk may have caused this difference. My thesis is divided into three studies (chapters two to four) and the objectives of each are described below.

In chapter two, I examine how New Zealand birds react to the presence of model predators at their nests. I aimed to determine if mainland native birds, exposed to kiore for at least 700 years and to other mammalian predators for around 130 years (King 1984; Worthy & Holdaway 2002), have developed the ability to recognise mammalian predators such as stoats (*Mustela erminea*) as a threat. I also aimed to determine if anti-predator responses disappear for birds in the absence of predators, such as with introduced birds and snakes (a predator which they coevolved with in their native ranges, but is not present in New Zealand). I placed models at the nests of birds in order to observe their reaction so I could determine if they were recognising each model as a threat.

In chapter three, I examine the difference in predator recognition between mainland South Island robins (*Petroica australis*) (which are sympatric with mammalian predators) and island robins (where they have never experienced mammalian predators). I aimed to determine if robins on the mainland had adapted to mammalian threats, by observing how a naïve population responds. I hypothesised that mainland robins would react as strongly towards the stoat as they do towards a model morepork (*Ninox novaeseelandiae*), a native predator, but that the island robins would not. Once again, I placed models at the nests of robins in order to observe their reaction so I could determine if they were recognising each model as a threat.

In chapter four, I investigated whether or not South Island robins had consistent personalities on the bold-shy trait continuum and whether personality varied between two populations with differing predation risks. I hypothesised that selection pressures on mainland birds (exposed to predators) would have made them shyer on average than island birds (with no selection against being bold). I tested this by placing mealworm larvae (*Tenebrio molitor*) on the ground near a human researcher (which I considered to be a risky situation) and observing whether the robin approached or not and by measuring the time it took to approach and remove the mealworms.

Finally, in the last chapter (chapter five) I review my findings and offer suggestions for future research. Overall, my studies help demonstrate how some species are not necessarily evolutionarily trapped and unable to change behaviour or personality traits when an exotic predator establishes. They may be able to adapt to the novel predators via a mixture of phylogenetic and ontogenetic influences.

Each chapter has been primarily written as an individual research paper, hence there is some repetition.

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CHAPTER TWO: RECOGNITION OF NOVEL PREDATORS

ABSTRACT

Studies have shown that some species or populations lose the ability to recognise and respond appropriately to predators from which they are geographically isolated. This ability can be regained but is likely to depend on length of geographical separation from a predator and whether or not other similar suites of predators are extant. New Zealand's native birds evolved in isolation from predatory mammals, which has lead to them becoming naïve to the threats these species pose. In this study, I used a series of model presentations to determine whether four species of native birds have the ability to recognise one of their introduced mammalian predators, the stoat (*Mustela erminea*), as well as a native predator (morepork, *Ninox novaeseelandiae*) and a novel predator that has not been introduced (snakes). I also compared the responses of four species of introduced European birds (which coevolved with predatory mammals and snakes in their native range) to the same series of models. Despite having only been exposed to stoats for *c.* 130 years, I found that some native species now recognise this predator, as indicated by an increased rate of alarm calling, swooping at the model and refraining from feeding their nestlings while the model was present. In contrast, neither native nor introduced birds responded to snake models at the nest, perhaps indicating that they have likely 'forgotten' snakes as a threat. As expected, all species tested reacted to morepork models. These results suggest some native birds have developed recognition of recently arrived novel mammalian predators while introduced birds have apparently lost the ability to recognise snakes as predators despite having formerly been sympatric with them in their native range. My findings have implications for reintroduction projects of native birds, where island or captive-bred birds are translocated into areas containing mammalian predators. If individuals have lost their anti-predator behaviours, translocated populations

may be more at risk of decline, depending on the rate of learning or adapting. My results also suggest the likely negative consequences if snakes ever become established in New Zealand.

INTRODUCTION

Nest predation is the single greatest cause of reproductive failure in most birds (Montgomerie & Weatherhead 1988). Therefore, selection pressure on birds to reduce the risk of nest predation is likely to be strong (Ricklefs 1969; Martin 1993; Martin 1995). Predator recognition is an important part of avoiding predation. To defend a nest, birds must first be able to accurately identify threats. Wrongly doing so may result in either a nest being depredated or energy and time being wasted by responding to something which is not a threat. However, if selection pressure from predation is relaxed, as can happen with a species becomes geographically isolated from predators, then the ability to recognise and respond appropriately may be lost due to the cost of maintaining anti-predator adaptations when they bring no benefit. Species that evolved in the absence of some predator guilds, are thought to be particularly vulnerable to exotic predators (Salo et al. 2007) and may lack recognition altogether due to their long period of isolation.

Whether a species that is isolated from its predators continues to recognise a predator may depend on its evolutionary history (Lima & Dill 1990; Blumstein & Daniel 2005; Stankowich & Coss 2006; Beauchamp 2010). If one predator is lost but other similar species remain (*e.g.* loss of one species of owl but contact with a new species of owl), recognition is unlikely to diminish as anti-predator adaptations against one species may be just as effective against other predatory species in the same guild. However, if no similar predators remain in sympatry, then anti-predatory adaptations are more likely to be lost (Blumstein 2006). Reacting falsely to a non-predator can be costly, as it may diminish time and energy that is better spent on other behaviours such as foraging or parental care (Blumstein et al. 2000; Verdolin 2006). The higher the cost of maintaining anti-predator behaviours in the absence of the predator, the faster behaviours should be lost. Behaviours are also more likely to be lost over a shorter time frame if the behaviour is experience dependent (*i.e.*, learnt) but is more

likely to persist if it is 'hard-wired' or has a genetic basis (Blumstein 2002). Alternatively, anti-predator behaviours may be more easily regained if they are experience dependent, if the animal possesses a general anti-predator strategy, or if other similar predators are still present.

Some animals have been shown to be able to identify predators at a young age, without any learning from parents or from having experienced a predatory event. For example, naïve, hand-raised pied flycatchers (*Ficedula hypoleuca*) (Curio 1975) and naïve Seychelles warblers (*Acrocephalus sechellensis*) (Veen et al. 2000) appear to innately recognise their predators through visual cues. Other studies have shown that naïve animals can show anti-predator responses when exposed to the odour of a predator (Fluck et al. 1996; Monclús et al. 2005; Zidar & Løvlie 2012). Such innate recognition has been found to persist despite periods of isolation (Blumstein 2006; Schel & Zuberbühler 2009; Placyk & Burghardt 2011; Zheng et al. 2013). In other cases, animals have been shown to require experience-based learning in order to identify predators. For example, blackbirds (*Turdus merula*) learned to fear a harmless model when witnessing a conspecific seemingly acting aggressive towards it, whereas control blackbirds without a teacher remained unresponsive (Curio, Ernst & Vieth 1978). Other species retained differing levels of recognition. For example, tammar wallabies (*Macropus eugenii*) which had been isolated from mammalian predators for 9500 years on offshore islands around Australia, responded to taxidermic models of mammalian predators but not to their audio recordings (Blumstein et al. 2000). Finally, some animals appear to lack the ability to recognise and respond appropriately to certain predators. This appears to be most common where a species has been isolated from entire predatory guilds, such as on islands. The longer the period of isolation and the fewer suites of extant predators, the more likely behaviours are to be lost (Blumstein & Daniel 2005). A study showed that the endemic takahe (*Porphyrio mantelli*) (which has evolved in isolated from mammalian predators) did

not respond as strongly to a taxidermic stoat in comparison to the non-endemic pukeko (*Porphyrio porphyrio melanotus*) (which has a more recent history of evolving in conjunction with mammalian predators) (Bunin & Jamieson 1996). Likewise, Leach's storm petrels (*Oceanodroma leucorhoa*) lacked the ability to recognise or respond to a novel predator, the great skua (*Stercorarius skua*) and were being depredated at unsustainable levels (Miles et al. 2013).

New Zealand provides a perfect setting to investigate how previously naïve populations of island birds respond to novel predators and how their response varies with experience as populations of some species co-occur with novel predators. Previous studies have shown that some native bird species have gained or lost anti-predator behaviours within short generational time frames (Massaro et al. 2008; Jamieson & Ludwig 2012), suggesting the ability to recognise novel threats is not fixed and some species and populations may be able adapt to new predatory regimes. There are also a range of exotic birds which were introduced upon European settlement (primarily in the late 19th century). Many of these introduced species have escaped some of their natural predators from their native ranges, including snakes. It is possible that introduced birds do not recognise or react to snakes, due to innate traits being lost or not having had an experience of them. However, it is also possible that they have retained a genetic ability to recognise them, despite the long period of isolation, if such recognition has a genetic basis and low cost. The objective of this chapter is to determine how New Zealand birds respond to novel predators. I predicted that both native and introduced birds would respond to the morepork (*Ninox novaeseelandiae*) and stoat (*Mustela erminea*), although natives might be expected to respond to a lesser extent to the stoat in comparison to the morepork given the differences in time they have occurred in sympatry. If predator recognition is innate I predicted that native birds would not respond to the snake while introduced birds would.

METHODOLOGY

STUDY SITES

I studied the response of birds to different types of predators in a native forest near the town of Kaikoura on the South Island. Bird nests were studied in two forest patches, one at Kowhai Bush (-42.376,173.616) and another at Waimangarara Bush (-42.341,173.659). Kowhai Bush is approximately 240 ha in area and is dominated by kanuka (*Kunzea ericoides*). The understory is composed of various native and introduced shrubs. For a more detailed description, see (Hunt 1979). Waimangarara Bush is approximately 65 ha in area and located approximately 5 km to the north of Kowhai Bush. It is composed of similar vegetation and holds a similar diversity of bird species. The two sites are joined through a continuous band of montane forest at their western edges but are otherwise separated by farmland. Kowhai Bush receives little predator control, and this primarily targets possums via baits and traps around the perimeter. Waimangarara Bush had been subject to more extensive predator control prior to this study; however, pest control efforts were similar to that of Kowhai Bush during this study (Barry Dunnett, *pers. comm.*). There was no significant difference between Kowhai Bush and Waimangarara Bush ($p > 0.05$), in the analysis so these were combined into one location. Introduced mammalian predators that are present at the sites include feral cats (*Felis catus*), stoats, (*Mustela erminea*), ferrets (*Mustela putorius furo*), weasels, (*Mustela nivalis*), rats (*Rattus rattus* and *R. norvegicus*), mice (*Mus musculus*) and possums (*Trichosurus vulpecula*).

STUDY SPECIES

A variety of native and introduced passerine bird species were tested. Native species included South Island robin (*Petroica australis* - Toutouwai), New Zealand fantail (*Rhipidura fuliginosa* - Piwakawaka), grey warbler (*Gerygone igata* - Riroriro) and rifleman (*Acanthisitta chloris* - Tītipounamu). Introduced species included song thrush (*Turdus*

philomelos), common blackbird (*Turdus merula*), common starling (*Sturnus vulgaris*), and silvereye (*Zosterops lateralis* - Tauhou). While silvereyes are literally considered a native species due to their naturalised arrival to New Zealand, for the purpose of this study they were grouped with the introduced birds as they only arrived in the 19th century from Australia, and share a recent co-evolutionary history with predatory mammals that is more similar to that of introduced European birds than with the other native birds of New Zealand.

Nests were typically located by searching the vegetation or following parent birds. Nest boxes were provided for riflemen and starlings within Kowhai bush. As both species appear to prefer boxes over natural sites, these were used in the study. Nests were monitored until the nestlings were at the pin-break stage of development, at which point model presentation experiments were conducted (see next section). This age was chosen to control for differences in the nestling period across species, as the different species develop at different rates. It was important to use a consistent stage because defence intensity has been shown to increase during the nesting cycle (Knight & Temple 1986). Using this stage also minimised the risk of the parent birds abandoning the nest. It is possible that some of the same parents may have been tested repeatedly (during different nesting attempts), resulting in pseudo-replication. Where possible, measures were taken to avoid testing individuals more than once. Robins and rifleman on the study site could be identified by unique colour bands so individual's nests were never used more than once. Other species are usually territorial and re-nest within the same area or tree. Therefore, if a new nest appeared near a nest that already been filmed, it was not used for any further presentation experiments.

MODEL PREDATORS

Four types of models were used. Firstly, a cardboard box (95 x 95 x 185 mm) was used as a control to test whether parent birds could be reacting simply to the presence of a novel object in the vicinity of their nest. The second model was a taxidermic mount of a morepork (*Ninox*

novaeseelandiae - ruru), a non-novel predator (size is approximately 90 x 90 x 190 mm). This is a native predator, with which New Zealand endemic birds have coevolved. It was chosen to determine how a bird responds to a non-novel predator. The introduced species coevolved with similar looking species of owls in their native range and thus may perceive it as a threat. The third model was a taxidermic mount of a stoat (*Mustela erminea*) (230 x 30 x 40 mm). Stoats were established in New Zealand in 1885 (Worthy & Holdaway 2002), thus endemic species only have a short history of sympatry with these mammalian predators. In contrast, introduced birds and the recently arrived silvereye) have coevolved with mammalian predators in their native ranges, including mustelids such as stoats (or carnivorous marsupials in Australia for the silvereye). The fourth model was a rubber snake. Snakes have never established in New Zealand, therefore they are completely novel to the endemic and native bird species. Although introduced birds coevolved with snakes in their native ranges (including both European and Australian birds), they have not encountered them since their introduction to New Zealand over 100 years ago and thus may no longer recognise or perceive them as a threat. Two types of rubber snake models were used and they most closely resembled the red-bellied black snake (*Pseudechis porphyriacus*) (with two sized models, 190 x 190 x 45 mm and 150 x 130 x 20 mm) and the olive python (*Liasis olivaceus*) (150 x 130 x 20 mm). They were purchased from an Australian business which sells bird-scaring products (http://www.pestawayaust.com.au) and are said to be effective in scaring wild birds from food crops in Australia. All three of the animal predators are a threat to adults birds and their nests (Neal, Montague & James 1993; Murphy & Dowding 1994; Haw, Clout & Powlesland 2001; Weatherhead & Blouin-Demers 2004; DeGregorio et al. 2014).

MODEL PRESENTATIONS

Model presentation was carried out during the spring/summer nesting season between

September and January in 2012-13 and 2013-14. All presentations were filmed by placing a camera mounted on a tripod approximately 5 – 10 m from the nest. Filming started between 6 am and 9 am (NZST). Each nest was filmed for a control period of one hour. The researcher then approached the nest while the parent was absent and positioned a randomly selected model approximately 0.5 m from the nest. The model was placed facing towards the nest in a neutral pose. The researcher then left the vicinity and watched or listened for the parent's return. For native species, which are more likely to return to the nest in the presence of humans (*pers. obs*.), the researcher could be within 15 m of the nest. For introduced species, the researcher had to retreat out of sight (> 15 m) and relied primarily on listening for alarm calls to signal the return of the parents to the nest. After 3 minutes the model was removed. If the parent was not seen or heard within 15 minutes after placement, the model was removed. After 1 hour the process was repeated with another model, until all 4 had been presented in a random order (but without testing the same model twice). The filming continued for 1 hour after the removal of the fourth model. Written notes were taken regarding the parents' reactions to the models and later compared with the video recordings. The parents' behaviour before the presentations was also analysed to determine the behavioural pattern of a normal visit to the nest without a model.

BEHAVIOURS

A variety of behaviours were used to determine if a bird reacted to the model predator. Three of these were chosen to illustrate how the birds reacted to the models. Firstly, the number of alarm calls during the first minute was counted from the video recordings. Alarm calls were defined as the vocalisations each species made when distressed and did not include other vocalisations such as contact calls, singing or begging. Secondly, whether the model was attacked by swooping was recorded. Swooping was defined as when the parent repeatedly flew or hopped close to the predator. Thirdly, I recorded whether birds fed their young during

the model presentation. Lack of feeding was defined as when the bird did not feed the nestlings. Feeding elicits begging calls from offspring, so if a bird recognises a threat, it should not feed its young, in order to avoid attracting the attention of the predator. These behaviours (*i.e.*, alarm calling, swooping, and not feeding) suggested that the parent birds perceived the model as a threat.

STATISTICAL ANALYSIS

Linear models were used on each species for each behaviour to compare differences between the control no-model period and the predator presentations. A Poisson distribution was used for the alarm call data and a binomial distribution was used for all other behaviours. A critical value of 0.05 was used in all tests. Statistical analyses was performed using the program RStudio, version 0.98.501.

RESULTS

A total of 84 nests were tested over the two seasons. This included the nests of 14 blackbirds, 9 silvereyes, 19 song thrushes, 8 starlings (Introduced species, figure 1) and 6 grey warblers, 10 fantails, 10 rifleman and 8 robins (Native species, figure 2).

The general response to the box did not differ to that of the control no-predator treatment. Rifleman were the only species that alarm called significantly more to the box than to the control ($p = 0.006$) and were also the only species that had a significantly higher percentage that swooped ($p < 0.001$) (figure 2). However, their alarm call rate and swooping percentage for the box was still significantly less than for the morepork and stoat ($p < 0.001$) suggesting they did not necessarily view the box as serious a threat as a predator. Blackbirds were the only species that tended to feed their chicks at a significantly lower rate than during the control ($p = 0.008$) (Figure 1).

All eight species appeared to recognise the morepork as a threat. Their reaction to the morepork was significantly different to the control no-model treatment ($p < 0.05$). All species alarm called more and had a higher percentage that swooped and that did not feed their nestlings ($p < 0.05$) (figures 1 & 2).

Similar to the morepork, all species appeared to recognise the stoat as a threat. All eight species had a significantly higher percentage that swooped and that did not feed nestlings in comparison to the control ($p < 0.05$) (figures 1 & 2). Seven of the species alarm called significantly more than for the control ($p <0.05$). Robins were the only species that did not alarm call at a significantly greater rate ($p = 0.41$). However, the difference in calling between the morepork and stoat was not significant ($p = 0.22$), suggesting this species may only alarm call at a low rate when faced with any intruder or object near its nest (figure 2).

The snake did not appear to be recognised as a predator. Rifleman were the only species that alarm called significantly more to the snake than during the control ($p = 0.004$), but it was still less than they called during the morepork presentation. Rifleman and blackbirds were the only species which had a lower percentage feed their chicks, though rifleman fed more than when the morepork or stoat was present ($p < 0.001$). Rifleman, silvereyes and starling all had a significantly higher percentage that swooped at the snake compared to the control ($p < 0.05$). However, a higher percentage of rifleman swooped at the morepork and stoat.

DISCUSSION

The general pattern shown in the results is that all the species tested recognised moreporks and stoats as a threat to their nests but not snakes. This is shown by the increased number of alarm calls and anti-predator behaviours and decreased parental care behaviours when the model morepork or stoat were present in relation to the controls. This suggests that these

native New Zealand birds have been able to adapt to a novel predator, the stoat. It also suggests that these introduced birds have lost the ability to recognise snakes as a predator.

Reaction to the cardboard box in general did not significantly differ from the control no-model period. For the species or individuals (such as rifleman) that reacted, they may have an advantage if novel predators do establish in New Zealand, since they appear to react to any novel item near their nest. The box may have been too novel, since square corners and straight edges are uncommon in natural settings. However, this seems unlikely, as all of the rifleman tested were nesting in nest boxes (with other unoccupied boxes scattered in the field sites). It does not make sense for a bird to react too strongly to a sudden physical change in the immediate environment otherwise they might abandon clutches unnecessarily. For the species that did react, their response was less intense than to the actual predators and usually only one behaviour differed from the control, whereas the response to predator models were more consistent for all behaviours.

The taxidermic mounts of the morepork generally provoked aggressive or defensive behaviours. This is unsurprising as native species have evolved with moreporks, as well as other species of owl (including the introduced little owl *Athene noctua* and the recently extinct and endemic laughing owl *Sceloglaux albifacies*). Similarly, introduced European birds species have evolved with a wide range of owl species in their ancestral origins (and the ancestors of silvereyes evolved with a number of owls in their native Australia). None of the bird species in my study have experienced isolation from owls thus recognition continues to persist and given the relative conservative and similar appearance of owls, it may be relatively easy for birds to recognise and respond to all or most species of owl.

The taxidermic mount of the stoat also provoked nest defence behaviour and generally appeared to be recognised. This is unsurprising for introduced species, as they have co-

evolved with stoats and other mammalian predators in their native ranges. The native New Zealand species tested also appeared to recognise the stoat. This could be due to three reasons. Firstly, they may have a general anti-predator reaction for any unfamiliar animal at the nest. Native species have evolved with avian predators and this may have helped them maintain their anti-predator response, such as suggested by Blumstein (2006). Secondly, they may have evolved to recognise stoats. As nests experience very high predation rates by introduced mammals (Brown 1997), selection pressures should be expected to be act relatively quickly and favour individuals that responded appropriately. Thirdly, they may be experience dependent and need to have a near miss or witness other birds reacting negatively in order to recognise stoats. Social learning can play an important part of predator avoidance. For example, mice (*Mus musculus*) that witnessed conspecifics being attacked by biting flies (*Stomoxys calcitrans)* learnt to display avoidance behaviour without having encountered the flies themselves (Kavaliers, Colwell & Choleris 2003) and naïve robins were able to be trained via witnessing conspecifics reacting to various models (McLean, Hölzer & Studholme 1999). These hypotheses are not mutually exclusive and all may have played a role in developing defences against exotic predators. Other studies have also shown that some species are not evolutionary trapped when environmental change occurs (such as introduction of novel predators) and have been able to adapt to exotic predators in relatively short time periods (Carthey & Banks 2012; Anson & Dickman 2013).

None of the tested species appeared to visually recognise immobile rubber snakes as predators. This study, however, did not address other sensory channels that may aid in predator recognition. The rubber snakes may not have looked or smelt like a real snake, whereas the taxidermic morepork and stoat at least retained the natural plumage and fur. Olfaction has shown to be important for birds in detecting risk (Amo et al. 2008). However, studies on predator recognition based on olfaction have had mixed results (Godard, Bowers &

Morgan Wilson 2007; Amo et al. 2008; Zidar & Løvlie 2012; Forsman et al. 2013) and olfaction may be more important to hole nesting birds, where the parent cannot see into their nest and thus relies on odours. The model snake was also not moving (although neither were the taxidermic mounts of the morepork and stoat and they still elicited responses). Snakes tend to be sit-and-wait ambush predators (Lourdais, Gartner & Brischoux 2014), so relying on movement alone to detect their presence would not be effective. The rubber snakes may not reflect light and in the same way that a real one would. Thus, it is possible that the appearance of snakes was not real enough to be recognised as anything more than simply a novel object. However, other studies involving artificial snakes have shown that a variety of species do respond (Mitrovich, Cotroneo & Edwards 2006; Koboroff, Kaplan & Rogers 2013; Etting, Isbell & Grote 2014). Anecdotally, a young pet Australian Magpie (*Cracticus tibicen*) in New Zealand reacted strongly to toys and even candy snakes (Brockie & Sorenson 1998). These examples support the use of an artificial snake as a suitable model. Thus, the artificial nature of the model I used is unlikely to be the cause of the lack of reactions.

There are no similar predators to snakes in New Zealand and isolation from them may have caused introduced birds to 'forget' how to recognise and respond. Anti-predator behaviour can be considered costly, so if it is unneeded, it is may be lost through selection pressures (Blumstein & Daniel 2005). This can occur despite relatively short isolation times, as other studies have shown. For example, tammar wallabies also lost anti-predator behaviour in a similar time frame of 130 years (Blumstein, Daniel & Springett 2004). Alternatively, recognition of snakes may be a learnt behaviour, either from parents or other birds. In the absence of snakes, such "training" would be lost within a generation. It would be interesting to know whether the loss of recognition of snakes occurs rapidly in recently introduced populations (suggesting a learnt response) or if it is more gradual and the product of selection against an adaptation that is no longer needed and costly to maintain.

FUTURE STUDIES

In order to determine if nest defence behaviour is learnt or genetic, this study could be repeated across several seasons on individually-identified birds (*e.g.*, colour-banded robins or rifleman). This data could be used to see if age and presumably experience are important factors in the ontogeny of predator recognition. If some species of birds need experience to learn the identity of their predators (*e.g.* stoats), this could explain why some individual birds did not appear to react strongly. For example, I noted that one pair of robins tested were raising their first clutch (as they had been colour-banded as fledglings the prior year) and they did not utter alarms for any of the presentations, suggesting they had not yet developed the same level of nest defence behaviours as older birds. This data would also give the opportunity to conduct repeatability estimates to see if individuals are consistent in their nest defence behaviour.

This study could also be repeated in Australia to see if the rubber snakes were recognised by birds that currently live and have evolved with snakes. Where possible, the same species could be used, or if not, ones from the same genus. This would confirm whether the rubber snakes were a realistic substitute for live snakes. The study could also be repeated in New Zealand with a taxidermic model of a snake, in order to match the other predator models. It would also be interesting to explore how other senses affect predator recognition and a bird's reaction. This could be done by making use of each predator's urine and mechanically enabling movement and sound in the models.

CONSERVATION IMPLICATIONS

It is concerning that New Zealand birds lack recognition of snakes. It is certainly not implausible that snakes (or other exotic reptiles or amphibians) may establish here via accidental introduction in the future. There are already numerous instances of live snakes being found post-border (Gill, Bejakovich & Whitaker 2001) and instances appear to be

increasing, due to increased trade. There have already been cases of brown tree snakes (*Boiga irregularis)* reaching New Zealand. Studies have predicted that they could survive in certain habitats in the northern parts of the country (Rodder & Lotters 2010). This highly invasive snake is responsible for causing significant declines in Guam's birds, lizards and small mammals (Savidge 1987; Rodda, Fritts & Chiszar 1997; Wiles et al. 2003). New Zealand has similarities with Guam that could also result in such tragedy – this generalist snake has no competitors and few predators in either location, it can cope with environmental stress and changes and introduced rats provide it with an alternate food source when birds become scarce. Both locations have native avifauna that are evolutionary naive to such a predator. Hence it is likely that if snakes ever establish in New Zealand, both native and exotic bird populations would be greatly compromised. This study stresses the need for continued and improved biosecurity efforts in New Zealand

It is reassuring that some native birds appear to recognise stoats as this species (and other mustelids) are considered to be a significant predator of New Zealand forest birds, along with rats (Brown 1997). Unfortunately, other species of native species presumably did not adapt and thus are now located only on offshore, predator-free islands. It is doubtful they will ever adapt and translocations to unprotected mainland areas are unlikely to be successful unless they also could learn or adapt to these exotic mammalian predators. Length of isolation may be the key predictor in whether naïve island birds will ever develop the ability to recognise novel predators (Blumstein & Daniel 2005). Population size is also an important factor, as lower populations often have reduced genetic diversity and have been found to be more likely to lose anti-predator behaviours (McPhee & McPhee 2012). Alternatively, species that have been isolated from a predator for shorter time periods have been able to relearn to respond. For example, South Island robins (*Petroica australis*) were conditioned to show alarm behaviours toward model predators (McLean et al. 1999). There have been numerous other

examples where animals have been successfully trained (Van Heezik, Seddon & Maloney 1999; Griffin, Blumstein & Evans 2000; Azevedo & Young 2006; Teixeira & Young 2014). Overall, when considering translocation of populations from predator-free island or captivity, care should be taken to consider if predators have been ‘forgotten’ or not and if so, can they be retaught?

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FIGURES

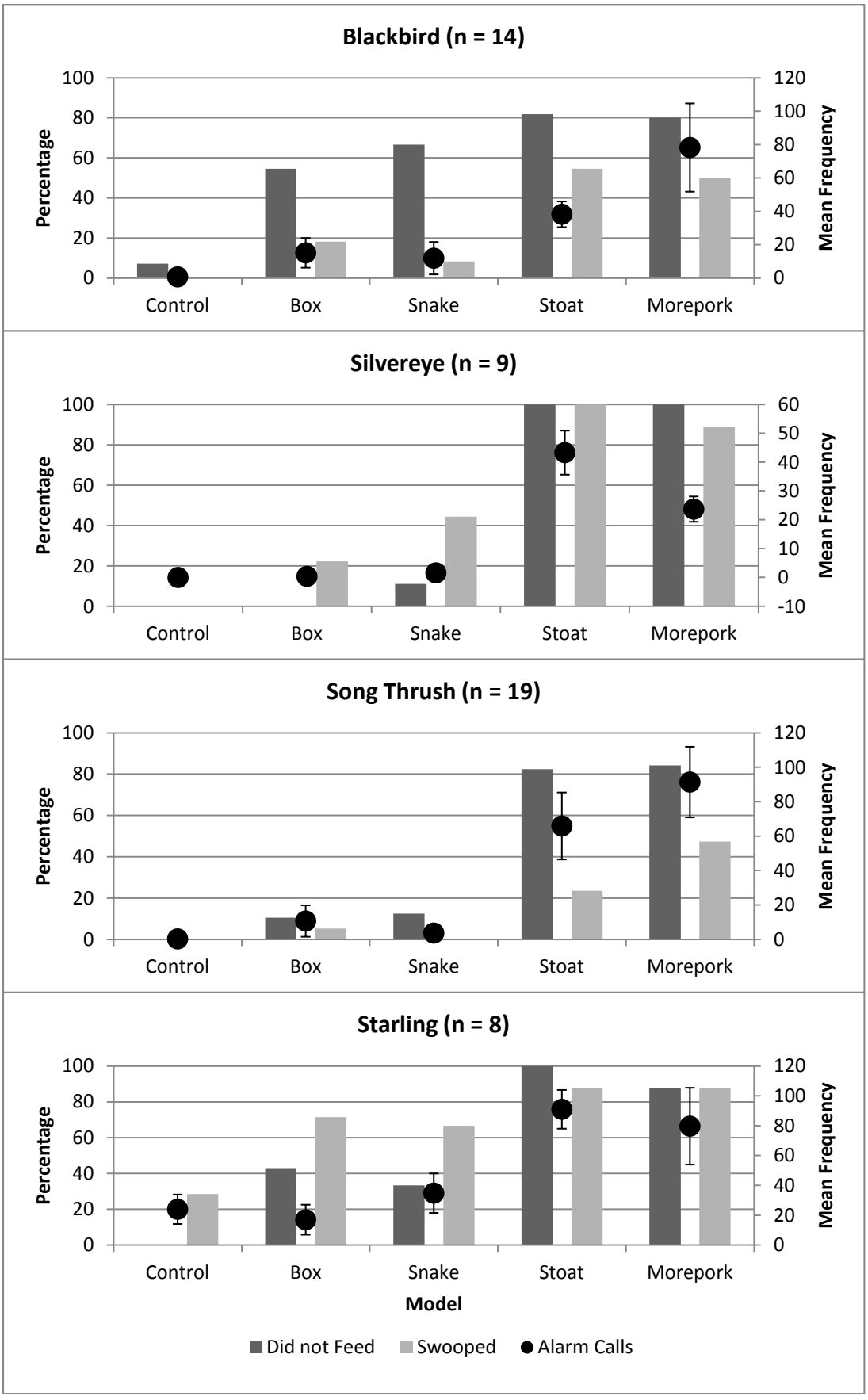
Blackbird (n = 14)
Percentage
Mean Frequency
100
80
60
40
20
0
120
100
80
60
40
20
0
Control
Box
Snake
Stoat
Morepork
Silvereye (n = 9)
Percentage
Mean Frequency
100
80
60
40
20
0
60
50
40
30
20
10
0
-10
Control
Box
Snake
Stoat
Morepork
Song Thrush (n = 19)
Percentage
Mean Frequency
100
80
60
40
20
0
120
100
80
60
40
20
0
Control
Box
Snake
Stoat
Morepork
Starling (n = 8)
Percentage
Mean Frequency
100
80
60
40
20
0
120
100
80
60
40
20
0
Control
Box
Snake
Stoat
Morepork
Model
Did not Feed
Swooped
Alarm Calls

Figure 1: Behaviours of three introduced bird species and a recent coloniser during model presentations. Bars denote percentage of nests where parents did not feed the nestlings and swooped towards the model. Dots denote the mean frequency of alarm calls during the first minute of the parent returning to the nest. Higher values suggest a more intense reaction while lower values suggest lack of recognition.

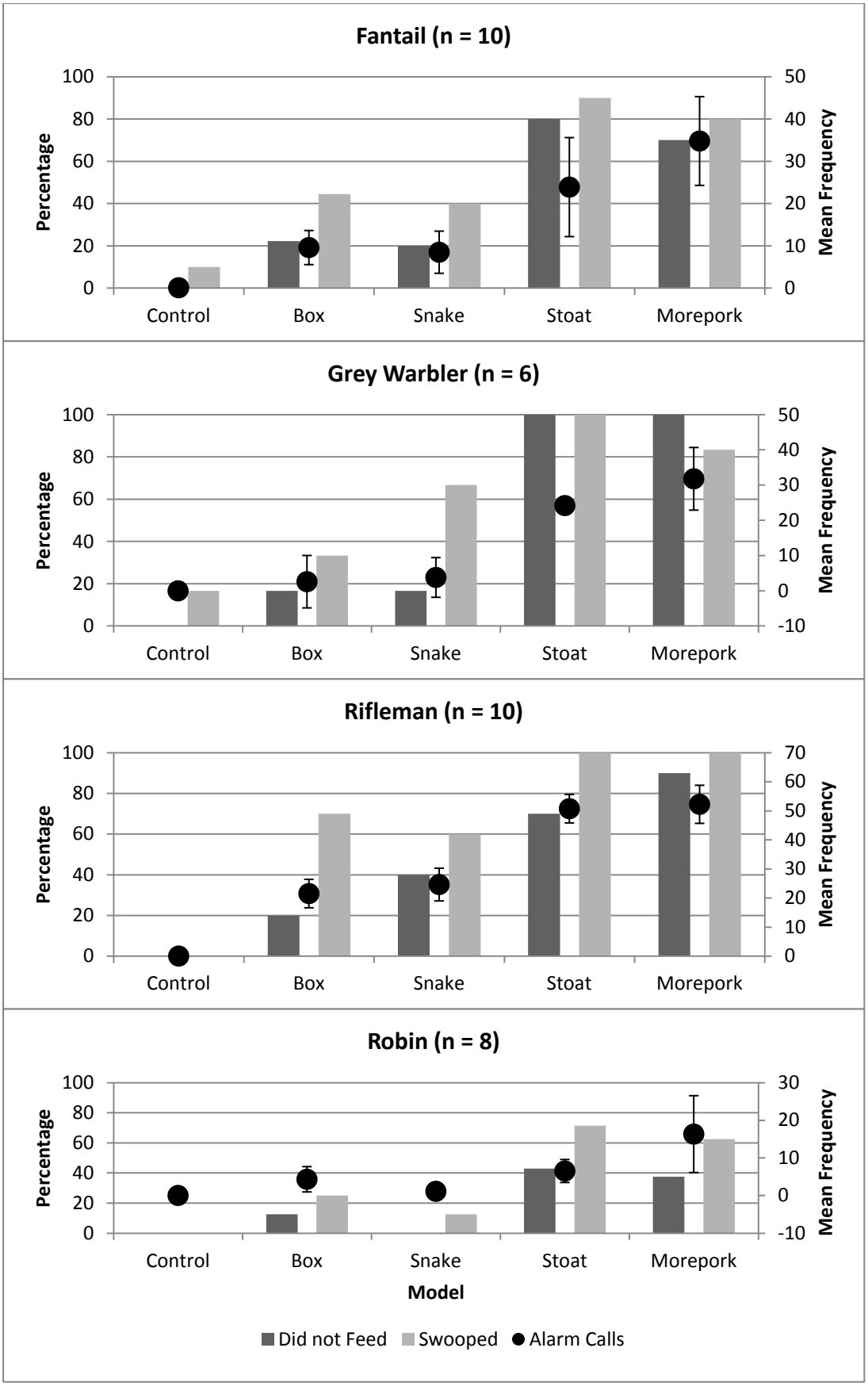
Fantail (n = 10)
Percentage
Mean Frequency
100
80
60
40
20
0
50
40
30
20
10
0
Control
Box
Snake
Stoat
Morepork
Grey Warbler (n = 6)
Percentage
Mean Frequency
100
80
60
40
20
0
50
40
30
20
10
0
-10
Control
Box
Snake
Stoat
Morepork
Rifleman (n = 10)
Percentage
Mean Frequency
100
80
60
40
20
0
70
60
50
40
30
20
10
0
Control
Box
Snake
Stoat
Morepork
Robin (n = 8)
Percentage
Mean Frequency
100
80
60
40
20
0
30
20
10
0
-10
Control
Box
Snake
Stoat
Morepork
Model
Did not Feed
Swooped
Alarm Calls

Figure 2: Behaviours of four native New Zealand bird species during model presentations. Bars denote percentage of nests where parents did not feed the nestlings and swooped towards the model. Dots denote the mean frequency of alarm calls during the first minute of the parent returning to the nest. Higher values suggest a more intense reaction while lower values suggest lack of recognition.

CHAPTER THREE: NOVEL PREDATOR RECOGNITION IN MAINLAND VS ISLAND SOUTH ISLAND ROBINS *PETROICA AUSTRALIS*.

ABSTRACT

New Zealand birds evolved in isolation from mammalian predators, causing them to lack some predator recognition abilities that are present in continental species. Comparing populations that differ in their exposure to predators can provide insight into how naïve populations of birds respond when encountering a novel predator. In this study, I compared two South Island robin (*Petroica australis*) populations, one sympatric with a range of invasive mammalian predators, and one population on a predator-free island, to determine how they behave when finding an introduced predator (stoat, *Mustela erminea*) at their nests. Reactions to a model stoat by robins in the island population did not differ from that of the control box while reactions to a model morepork (*Ninox novaeseelandiae*, an extant predator) were stronger, with more swooping and broken wing displays and less feeding of nestlings. This suggests robins allopatric with stoats do not perceive them as a threat to their nests. In comparison, the stronger response by robins on the mainland (sympatric with stoats) suggests they may be adapting to the introduction of exotic predators. The proportion of mainland robins that swooped, did broken wing displays and fed nestlings when the stoat was present did not significantly differ from that observed in the presence of the morepork model but did differ from the controls. This suggests that mainland robins perceive the stoat to be as much of a threat as the morepork. Although the mechanism by which mainland robins have developed the ability to recognise stoats is unknown, the lack of recognition of stoats by the island robins may be problematic if island populations are translocated onto the mainland for

conservation purposes. Translocations on the mainland may be more successful if source populations are used in which recognition of exotic predators has already developed.

INTRODUCTION

Island species are vulnerable to extinction, especially in relation to introduced exotic predators (Blackburn et al. 2004). Introduced mammalian predators are widely accepted as the leading cause of decline and extinction in the New Zealand avifauna (Diamond & Veitch 1981; Worthy & Holdaway 2002; Blackburn et al. 2004; Remeš, Matysioková & Cockburn 2012). Long periods of isolation have rendered many endemic species, including those in New Zealand, relatively naïve to predators that are common in continental avifaunas. The apparent loss of behavioural adaptations against some types of predators by island birds would certainly have added to their defencelessness when such predators were introduced by humans.

There have been a variety of studies that have identified behavioural differences in populations or species experiencing differing levels of predation risk (Van Schaik & Van Noordwijk 1985; Kavaliers 1990; Blumstein, Daniel & Springett 2004; Stankowich & Coss 2006; Peluc et al. 2008; Cooper Jr, Hawlena & Pérez-Mellado 2009; Brodin et al. 2012; Dingemanse et al. 2012). These differences may arise either by random evolutionary processes (*i.e.*, drift or founder effects) or via selection pressures from localized environmental factors (Bell 2005). In the case of relaxed selection, such as isolation from some predator guilds, it is apparent that costly predator recognition or defence traits can become diminished or lost (Lima & Dill 1990; Blumstein & Daniel 2005; Stankowich & Coss 2006; Beauchamp 2010). Absence of anti-predator behaviour is particularly common in insular species and populations, which can have tragic results when exotic predators establish (Blackburn et al. 2004). Alternatively, some species appear to have retained predator recognition (although this is sometimes less developed than in populations remaining sympatric with predators) despite varying periods of geographic isolation from a past predator (Beauchamp 2010; Anson & Dickman 2013). It is possible that the costs of

recognition were not high enough to be selected against, or other predators that may have been present were enough to maintain recognition for the absent ones.

Whether predator recognition (and an appropriate response) can be acquired by species that lack such ability is likely to be dependent on how long a species has been geographically isolated, if there are other similar predators present, if the species has a general anti-predator response to novel items, or a combination of all these factors (Blumstein 2006). For example, one study found that marine iguanas (*Amblyrhynchus cristatus*), which evolved without mammalian predators for a period of 5 – 15 million years, had not been able to regain recognition in the 150 years since mammals were introduced to the Galapagos Islands (Rödl et al. 2007) Another study found that presence of eagles (*Aquila audax*) was enough to maintain recognition of the extinct thylacine (*Thaylacinus cynocephalus*) in wallabies (*Macropus eugenii*) (Blumstein et al. 2000). There is also evidence that some species can be trained to recognise novel predators (Van Heezik, Seddon & Maloney 1999; Griffin, Blumstein & Evans 2000; Azevedo & Young 2006), which suggests that some degree of experience may be needed to develop recognition. The development of experience-based recognition may need to occur during a critical learning period while the individual is in a juvenile state although there is also evidence of adults being successfully trained (Van Heezik et al. 1999; Griffin et al. 2000; Azevedo & Young 2006). Furthermore, there is also emerging epigenetic evidence (albeit controversial) that the condition and experiences of the parents may alter whether genes are activated or not in their offspring. For example, stress hormones can be passed from mother to offspring, influencing their future behaviour (Sheriff, Krebs & Boonstra 2010; Morosinotto et al. 2013; Stratmann & Taborsky 2014), and this may play a role in predator recognition or avoidance.

New Zealand provides an opportunity to study differences in anti-predator behaviour between naïve island birds and birds that have now cohabitated with kiore (*Rattus exulans* –

Polynesian rat) for at least 700 years and with other mammalian predators for around 130 years (King 1984; Worthy & Holdaway 2002). Prior to human arrival, there were no terrestrial mammalian predators in New Zealand, so the bird species present are evolutionarily naïve to this guild of predators although they did evolve with a range of avian predators. After human introductions of a variety of mammalian predators, some species became extinct or rare, only persisting on offshore islands while others were able to survive despite the novel predators (Worthy & Holdaway 2002). By studying a species which is present on both the mainland and offshore islands, it is possible to see if the mainland populations have been able to adjust to the new predators. Alternatively, some New Zealand species are closely related to congeners in Australia (Worthy & Holdaway 2002), and species that only colonised recently may retain a "memory" of mammalian predators from their ancestors. It is therefore possible that they have retained innate recognition of predators from their shared co-evolutionary history.

The objective of this chapter was to compare the response of a population of South Island robins (*Petroica australis*) on a mammalian predator-free island to another population of robins on the mainland (which are sympatric with mammalian predators). Robins are an ideal study species as they can easily be observed in the wild and survive in areas sympatric and allopatric with a range of invasive mammalian predators. Both populations are sympatric with owls (native predator) while neither has been exposed to snakes (potential predator still absent from New Zealand). I predicted that island robins would respond most strongly to the model morepork and not a control, stoat or snake whereas the mainland robins should respond strongly to both the morepork and stoat and not the control or snake.

METHODOLOGY

STUDY SITES

Kaikoura is located on the South Island. The response of robins to model predators was studied in two forest patches in this area, one at Kowhai Bush (-42.376,173.616) and another at Waimangarara Bush (-42.341,173.659). Kowhai Bush is approximately 240 ha in area and is dominated by kanuka (*Kunzea ericoides)*. The understory is composed of various native and introduced shrubs. For a more detailed description, see (Hunt 1979). Waimangarara Bush is approximately 65 ha in area and located approximately 5 km to the north of Kowhai Bush. It is composed of similar vegetation and holds a similar diversity of bird species. The two sites are joined through a continuous band of montane forest at their western edges but are otherwise separated by farmland. Kowhai Bush receives little predator control, and this primarily targets possums via baits and traps around the perimeter. Waimangarara Bush had been subject to more extensive predator control prior to this study, however, pest control efforts were similar to that of Kowhai Bush during this study (Barry Dunnet, *pers. comm.*). There was no significant difference between Kowhai Bush and Waimangarara Bush ($p > 0.05$), in the analyses so these were combined into one mainland location. Introduced mammalian predators that are present at the sites include feral cats (*Felis catus*), stoats, (*Mustela erminea*), ferrets (*Mustela putorius furo*), weasels, (*Mustela nivalis*), rats (*Rattus rattus* and *Rattus norvegicus*), mice (*Mus musculus*) and possums (*Trichosurus vulpecula*).

Motuara Island is a 59 ha offshore island located in the Marlborough Sounds (-41.093,174.271). Forest structure is similar to that at Kaikoura (Maloney & McLean 1995). The island has been mammalian-predator free since 1990 when Polynesian rats (*Rattus exulans*) were eradicated (Maloney & McLean 1995). Robins were introduced in 1973 from nearby Nukuwaiata Island (Taylor, Jamieson & Armstrong 2005). In contrast to the wide range of introduced mammalian predators present on the mainland study site, neither the source population on Nukuwaiata, nor the current descendent population on Moturara Island

has ever been exposed to any mammalian predators other than Polynesian rats for any of their evolutionary history, though even this predator is no longer present (Maloney & McLean 1995).

STUDY SPECIES

SOUTH ISLAND ROBIN *PETROICA AUSTRALIS* (TOUTOUWAI)

South Island robins (hereafter referred to as robins) are an endemic passerine forest bird. They are insectivorous and largely feed on the ground. Breeding pairs are territorial and the male feeds the nesting female while both parents feed their nestlings and fledglings. Breeding occurs between September and January and 2-3 clutches are produced per season (Powesland 1983). Robins are well known for appearing to be fearless and inquisitive around humans. Robins evolved without the presence of any mammalian predators until these species introduced by humans but co-evolved with avian predators such as falcons and owls.

MODEL PRESENTATIONS

Model presentation was carried out during the spring/summer nesting season between September and January in 2012-13 and 2013-14. A total of 16 nests were observed altogether, 8 at each location. Nests were typically located by searching the vegetation or following parent birds. Nests were monitored until the nestlings were at the pin-break stage of development, at which point model presentation experiments were conducted (see next section). This age was chosen to also minimise the risk of the parent birds abandoning the nest. It was important to use a consistent stage because defence intensity has been shown to increase during the nesting cycle (Knight & Temple 1986). Most of the adult birds at both Kaikoura and Motuara Island had prior experience with researchers and many had already been fitted with unique colour band combinations so that individuals could be identified. There was no repeat testing of the same individuals' nests.

All presentations were filmed by placing a camera mounted on a tripod approximately 5 – 10 m from the nest. Filming started between 6 am and 9 am (NZST). Each nest was filmed for a control period of one hour. The researcher then approached the nest while the parent was absent and positioned a randomly selected model approximately 0.5 m from the nest. The model was placed facing towards the nest in a neutral pose. The researcher then left the vicinity and watched or listened for the parent's return. Robins are unafraid and will return to their nest in the presence of humans, so the researcher could be within 15 m of the nest. After 3 minutes the model was removed. If the parent was not seen or heard within 15 minutes after placement, the model was removed. After 1 hour the process was repeated with another model, until all 4 had been presented in a random order. The filming continued for 1 hour after the removal of the fourth model. Written notes were taken regarding the parents' reactions to the models and later compared with the video recordings. The parents' behaviour before the presentations was also analysed to determine the behavioural pattern of a normal visit to the nest without a model.

Four types of models were used. Firstly, a cardboard box (95 x 95 x 185 mm) was used as a control to test whether robins could be reacting simply to the presence of a novel object in the vicinity of their nest. The second model was a taxidermic mount of a morepork (*Ninox novaeseelandiae* - ruru), a non-novel predator (90 x 90 x 190 mm). This is a native predator, with which robins have coevolved. It was chosen to determine how a robin responds to a non-novel predator. The third model was a taxidermic mount of a stoat (*Mustela erminea*) (230 x 30 x 40 mm). Stoats were established in New Zealand in 1885 (Worthy & Holdaway 2002), thus robins only have a short history of sympatry with these mammalian predators. The fourth model was a rubber snake. Snakes have never established in New Zealand, therefore they are completely novel to robins. Two types of rubber snake models were used and they most closely resembled the red-bellied black snake (*Pseudechis porphyriacus*) (with two

sized models, 190 x 190 x 45 mm and 150 x 130 x 20 mm) and the olive python (*Liasis olivaceus*) (150 x 130 x 20 mm). They were purchased from an Australian business which sells bird-scaring products (http://www.pestawayaust.com.au) and are said to be effective in scaring wild birds from food crops in Australia. All three of the animal predators are a threat to adult birds and their nests (Neal, Montague & James 1993; Murphy & Dowding 1994; Haw, Clout & Powlesland 2001; Weatherhead & Blouin-Demers 2004; DeGregorio et al. 2014).

BEHAVIOURS

A variety of behaviours were used to determine if a bird reacted to the model predator. Four of these were chosen to illustrate how the birds reacted to the models. Firstly, the number of alarm calls during the first minute was counted from the video recordings. Alarm calls were defined as the vocalisations each species made when distressed and did not include other vocalisations such as contact calls, singing or begging. Secondly, whether the model was attacked by swooping was recorded. Swooping was defined as when the parent repeatedly flew or hopped close to the predator. Thirdly, I recorded whether the parent performed broken wing display while facing the model. This was defined as when the parents feigned injury and tried to lure the model away from the nest. Fourthly, I recorded whether birds fed their young during the model presentation. Lack of feeding was defined as when the bird did not feed the nestlings. Feeding elicits begging calls from offspring, so if a bird recognises a threat, it should not feed its young, in order to avoid attracting the attention of the predator. These behaviours (*i.e.*, alarm calling, swooping, broken wing display and not feeding) all suggested that the parent birds perceived the model as a threat.

STATISTICAL ANALYSIS

The alarm call data was non-parametric and a Kruskal-Wallis test was used to determine if there was a difference in behaviours between predator presentations. Linear models with

binomial distributions were used to compare differences between each of the models for the latter three behaviours. The differences between Kowhai Bush and Waimangarara Bush were non-significant, so these locations were combined into a single mainland site at Kaikoura. A critical value of 0.05 was used in all tests. Statistical analysis was performed using the program RStudio, version 0.98.501.

RESULTS

RESPONSE TO PRESENTATIONS AT KAIKOURA

There was no significant difference in number of alarm calls in the first minute of each presentation in response to any of the models (Figure 1; Kruskal-Wallis = 6.84, df=4, p=0.15). The percentage of nests where the parents performed broken wing display was highest when the stoat was displayed (57%), followed by the morepork (50%) and box (29%). No displays were performed for the control and snake. The percentage of nests where the parents swooped at the model was highest for the stoat (71%) followed by the morepork (63%). There was some swooping toward the box (25%) and snake (13%) but none for the control. The percentage of nests where nestlings were fed was lowest during the presence of the morepork followed by the stoat, then box. All birds fed their nestlings during the control and snake period.

RESPONSE TO PREDATORS ON MOTUARA ISLAND

There was a significant difference in number of alarm calls in the first minute of each presentation (Figure 2: Kruskal-Wallis = 13.45, df=4, p=0.009). The percentage of nests where the parents performed broken wing display was highest when the morepork was displayed (63%). None performed this behaviour for the control, box or snake and only 1 individual did so for the stoat (13%). All parents swooped at the morepork (100%). Significantly fewer parents swooped at the stoat (38%), box (29%) and snake (13%) ($p<0.05$)

while none swooped during the control period. The percentage of nests where nestlings were fed was lowest during the presence of the morepork (63%). The percentage feeding during the snake and stoat (75% each) did not significantly differ from this ($p<0.05$), which in turn did not significantly differ from the control and box where all nests were fed ($p<0.05$).

DISCUSSION

The reactions I observed towards the model predators suggest that there is a difference between island and mainland South Island robins in their recognition of introduced predators. At Kaikoura, the difference in alarm calling, broken wing displays and swooping between the morepork and stoat was non-significant, while on Motuara Island it was significant. The difference between the control, box and stoat also tended to be more similar on Motuara Island. These results suggest that robins at Kaikoura recognise stoats as being as much of a threat as a morepork while the Motuara Island birds do not. The naïve island robins likely represent how this species would have been before mammals arrived in New Zealand, which shows that mainland robins have successfully learnt to identify these novel predators. This is unsurprising as although robins are endemic, they have closely related congeners throughout Australasia, suggesting they have not been isolated from mammalian predators for as long as many of the species in families endemic to New Zealand (Worthy & Holdaway 2002).

There was only a slight and non-significant difference between the morepork and stoat for parents which fed their nestlings. However, there was also no difference between the stoat and the control, box or snake on Motuara, suggesting the response may be slightly different to than at Kaikoura. It was also noticed that robins at both sites tended to land on the nest and feed their nestlings before noticing the model (*pers.obs)*, hence the high percentage which fed while the morepork was present. Robins do not seem to use alarm calls in nest defence (see chapter two), which may attract a predator's attention towards the nest. There was a lot of

variation in alarm calling, and more data would be helpful in understanding if this is linked with predator type. Unfortunately sample sizes were low due to time and resource constraints in gathering data, particularly on Motuara Island. A larger sample size may have resulted in a clearer pattern for both these behaviours. In this study, broken wing display and swooping appear to be the most accurate indication of their recognition. If it were to be repeated, other behaviours should also be noted, such as raising crest feathers, which would also suggest agitation and thus recognition (Powlesland 1980).

Several previous studies have also found differences between mainland and island robins in their responses to introduced predators. North Island robin (*Petroica longipes*) on Tiritiri Matangi were found to have no significant difference in response between a control cardboard board and a taxidermic model of a stoat, whereas, mainland Auckland populations, with no predator control, showed the same response to the model stoat as they did for a model morepork (Whitwell et al. 2012). Similar results were also shown in South Island robins (Maloney & McLean 1995). One study even showed that recognition of rats was lost after only one generation in the Stewart Island subspecies of robin (*Petroica australis rakiura*) (Jamieson & Ludwig 2012). Data is currently insufficient for determining how fast recognition may be regained in individuals translocated from islands to the mainland. Differences in predator recognition abilities between populations could be genetic, learned or a combination. Studies have shown that naive, captive raised animals can be trained to recognise predators (Van Heezik et al. 1999; Griffin et al. 2000; Azevedo & Young 2006; Teixeira & Young 2014). However, this is more likely to be achievable if the animal in question shares an evolutionary history with the predator or one similar. By having another similar predator, the animal is likely to already have an appropriate response mechanism, whereas it may behave inappropriately towards a completely novel suite of predators (Blumstein 2006). For example, remaining motionless on the nest may be an effective

response towards an aerial predator that relies on sight to detect prey but could be useless against arboreal predators with a good sense of smell. A study showed that robins responded more intensely to stoats after being played inter-specific alarm calls (McLean, Hölzer & Studholme 1999). This suggests that they have a degree of plasticity in how they respond to novel predators and that social learning, experience or epigenetic factors may be important in gaining predator recognition abilities.

There are other reasons why Motuara robins may have appeared to lack recognition towards the stoat. Firstly, this study only looked at visual senses in relation to detecting risk, but it is likely that a combination of senses (such as olfaction and hearing) are engaged in predator recognition (Blumstein et al. 2000; Elmasri et al. 2012). It may be that the presence of a static model is not a sufficient cue to alert the birds to the risk. However, all birds appeared to recognise the model morepork and mainland birds appeared to recognise the model stoat so this is unlikely to be the explanation. Secondly, competition for resources are likely to be higher as on Motuara Island as robin densities are around ten times greater than on the mainland (Mackintosh & Briskie 2005). It is possible that this causes them to take more risks than mainland robins, as hunger or low energetic state has been shown to increase risk taking behaviour (Verdolin 2006; David et al. 2012). Thirdly, individual personality may also play a role in how the robins act towards a risky situation. Animals from populations lacking in predators are often on average bolder than those from populations sympatric with predators (Brodin et al. 2012; Dingemanse et al. 2012; Miranda et al. 2013b). Bolder individuals tend to differ in behaviour from shy individuals in a risky situation (Sih, Bell & Johnson 2004; Reale et al. 2007). Motuara Island robins are bolder than mainland robins (see chapter four), so they may be displaying less caution when approaching their nests despite the presence of a threat. However, the fact that Motuara Island robins did still react significantly more toward the morepork suggests that the latter two explanations may only play a small role, if any, and

that lack of recognition due to isolation or inexperience is the foremost reason why reaction to the stoat is low.

FUTURE RESEARCH

If the Motuara robins are ever used as a source population for translocation, it is recommended that the translocated birds are monitored to determine predation rates, or have this model predator presentation test repeated on the original and future generations. It would be interesting to see if and how fast the new site's population learns to recognise novel predators and whether it happens in one generation and if it is carried on in future clutches. The results would lend evidence to the legitimacy of using island birds as source populations. As many studies of anti-predator training are short-term, it would also be interesting to repeat or develop predator training techniques such as in McLean et al. (1999) to see how well training works over a longer generational period.

Motuara Island is also occupied by European blackbirds (*Turdus merula)* and several nests were found but due to time and weather restraints they were unable to be filmed during this study. Blackbirds on the island appeared tamer and spent more time on the ground and alarm called less than those at Kaikoura (*pers. obs*.). Differences in behaviour have been found between captive raised rural and urban blackbirds, suggesting that their behaviour has a genetic basis (Miranda et al. 2013a). It would be interesting to repeat this model predator presentation experiment on Motuara to see if blackbirds have 'forgotten' stoats. Chapter 2 indicates that they do not react to model snakes, despite only a short period of isolation so it is possible that island blackbirds may no longer react to stoats. The experiment could additionally include urban populations, which also tend to be tamer than the bush population at Kaikoura (*pers.obs*.).

CONSERVATION IMPLICATIONS

There is a multitude of mammalian-predator free islands around New Zealand which act as native bird sanctuaries. Stoats are known to be able to swim distances of at least 1.5 km and possibly much further (King et al. 2014), having had been found on islands 3 km offshore. Therefore, birds on these islands, including Motuara (which is approximately 1.8 km from the nearest mainland), are vulnerable to stoat reinvasion. The lack of recognition could have severe consequences on the robin population if one or more stoats arrive onshore. Fortunately, there are predator tracking and trapping programs already in place and it is highly recommended that vigilance remains high.

Translocation from island or captive-bred populations is currently a popular method of sustaining or reintroducing mainland populations (Seddon, Armstrong & Maloney 2007). This alone may be an ineffective way of conserving New Zealand's native birds if their predator recognition abilities are degraded or lost. Research suggests that relaxed selection decreases success of reintroductions (McPhee & McPhee 2012). The naive birds or their descendants may be more prone to predation, meaning that the translocation is a waste of resources. This is not to say that translocation should avoid using island populations of birds. Moving island birds to predator-controlled areas (assuming the control is carried on long term) or 'mainland islands' with predator-proof fences could be a good way to improve genetic diversity in these populations (Boessenkool et al. 2006). Robins and some other birds also appear to have some degree of plasticity in their behaviour and may be able to adapt within a short time frame (Massaro et al. 2008; Jamieson & Ludwig 2012). It has also been suggested that predator-training naïve individuals can result in increased survival after translocation, though whether or not this teaching lasts long term or will aid future offspring (via learning from conspecifics or through epigenetic inheritance) remains to be seen (Maloney & McLean 1995; McLean et al. 1999; Griffin et al. 2000).

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FIGURES

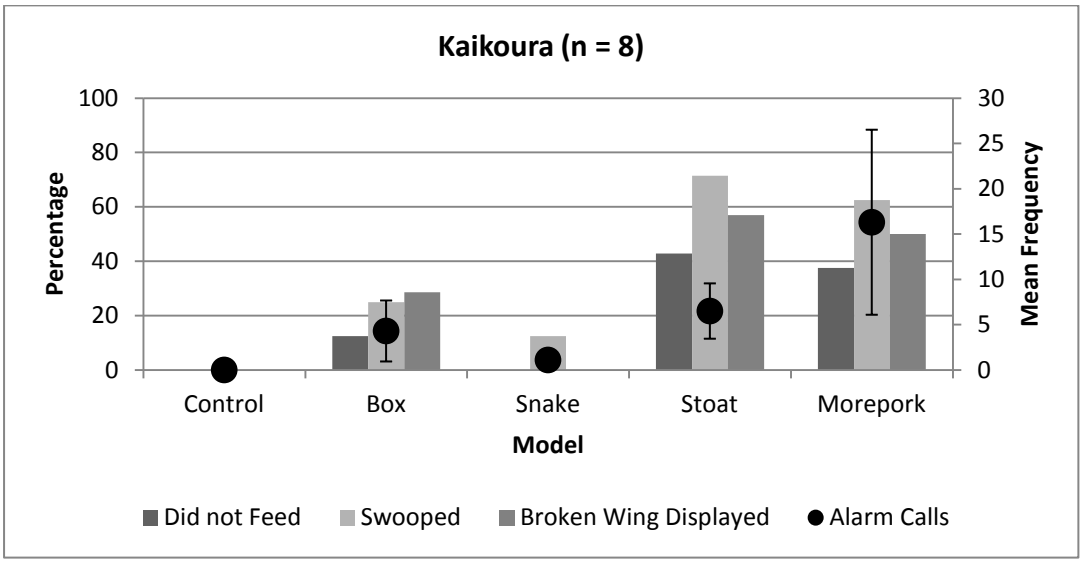

Figure 1. Behaviours of South Island robins at Kaikoura during 3 minute model presentations. Bars denote percentage of nests where parents did not feed the nestlings, swooped towards the model or performed broken wing displays directed at the model. Dots denote the mean frequency of alarm calls during the first minute of the parent returning to the nest.

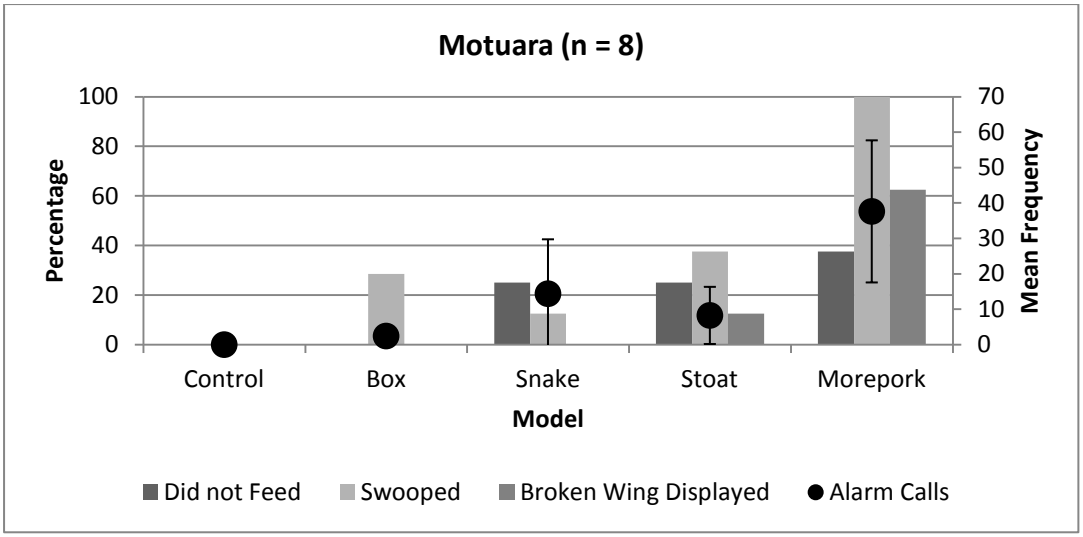

Figure 2. Behaviours of South Island robins on Motuara Island during 3 minute model presentations. Bars denote percentage of nests where parents did not feed the nestlings, swooped towards the model or performed broken wing displays directed at the model. Dots denote the mean frequency of alarm calls during the first minute of the parent returning to the nest.

CHAPTER FOUR: PERSONALITY DIFFERENCES BETWEEN MAINLAND AND ISLAND SOUTH ISLAND ROBINS (PETROICA AUSTRALIS)

ABSTRACT

Personality refers to the consistent difference in behaviour among individuals. Personality dimensions such as the boldness-shyness continuum have been described in a variety of species. Differing environmental conditions are likely to select for different personalities, meaning that two populations experiencing different rates of predation would possibly have different levels of boldness, due to the increased risk of being 'fearless'. In this study, I compared two populations of the South Island robin (*Petroica australis*), one of which is currently sympatric with a range of introduced mammalian predators (Kaikoura mainland population) and one of which has no introduced predators (Motuara Island population). I found that the robins on Motuara Island were generally bolder than mainland robins living near Kaikoura. This was evidenced by their increased willingness and faster times to approach a researcher in order to receive a food reward. Motuara Island robins were more likely to approach as close as 30 cm, 100 cm and 300 cm. They were also faster than Kaikoura robins in their initial latency and total times to remove five mealworm larvae from in front of a researcher. These differences may be due to bolder individuals having a fitness advantage on the island, perhaps because they can compete more effectively, while shy individuals may have the advantage on the mainland as it enables them to avoid predation. If these personality differences are at least partly genetic, the use of "bold" island birds as source populations for reintroduction to the mainland may be less effective than those using "shy" individuals from other mainland populations.

INTRODUCTION

The study of animal personality is a topic of current interest for behavioural scientists. Personality refers to consistent differences in behaviour between individuals (Sih, Bell & Johnson 2004; Reale et al. 2007; Brodin et al. 2012). This has also been referred to as coping styles or temperament or behavioural syndromes (Reale et al. 2007). A number of species have been shown to exhibit a variety of consistent personality traits (Gosling & John 1999). Although personality is often considered on an individual level, it can also be applied to different scales, such as when comparing two populations (Reale et al. 2007). One of the commonly studied personality types is "Shyness-Boldness," defined as an individual's reaction to a risky but not novel situation. Bold individuals tend to be less risk aversive than shy individuals, and spend more time doing risky activities such as basking or foraging in risky habitats (Carter, Goldizen & Tromp 2010; Carter et al. 2012b; Beckmann, Biro & Wright 2013) whereas the opposite is true of shy individuals. This trait should be considered as a continuum rather than bimodal, though individuals can exist at the extreme ends as tendencies. Individuals should also be relatively consistent in their place on the continuum, though this may change with environmental conditions, season and age or life stage (Reale et al. 2007).

The degree of boldness-shyness in an individual's personality can have an effect on its behaviour in a variety of different ecological contexts, such as in foraging (Bergvall et al. 2011), nest defence (Burtka & Grindstaff 2013), aggression (Bell & Sih 2007) and tameness (Barnett et al. 2013). Multiple personality tendencies (*i.e.*, both bold and shy individuals) may be able persist in a population due to tradeoffs. However, if conditions change or differ, directional selection can favour one personality tendency, causing it to become more prevalent over time.

Predation and fear of predation have been shown to select for changes in morphological traits in a variety of studies (Preisser, Bolnick & Benard 2005; Cresswell 2008). Predation risk is also likely to select for personality traits, especially if different traits alter the risks of being depredated (Quinn & Cresswell 2005). For example, bold and non-docile bighorn ewes (*Ovis canadensis*) were less likely to experience predation by cougars (*Puma concolor*) (Réale & Festa-Bianchet 2003). Similarly, the pups of active and aggressive female red squirrels (*Tamiasciurus hudsonicus*) were faster growing and survived better (Boon, Reale & Boutin 2007). Similar patterns are seen in domestic animals as well (Dugatkin 1992; Korhonen & Niemelä 1996; Hemsworth et al. 1999; Janczak et al. 2003; Smith & Blumstein 2010; Madden & Whiteside 2014). Differences in predation risk have the potential to select for or against certain personality traits, although the most advantageous traits are likely to differ for different species and situations. The difference in predation rates on individuals with different personalities may be due to different levels of activity (thus attracting a predator's attention), differences in length of time spent in riskier habitats, or greater willingness and less fear when exploring or approaching novel stimuli (Sih et al. 2004).

If personality traits provide benefits in relation to avoidance of predation, it is likely that two populations experiencing different levels of predation risk would also have differences in their average personality traits. Indeed, it has been found that personality traits often exhibit geographical variation (Foster 1999). For example, tadpoles and froglets of the common frog (*Rana temporaria)* found on islands were bolder and faster explorers when compared to their counterparts on the mainland where they were subjected to greater rates of predation (Brodin et al. 2012). The same pattern has been found in tadpoles in different ponds experiencing different rates of predation (Richardson 2001). Sticklebacks (*Gasterosteus aculeatus)* similarly had differing activity and aggressiveness levels depending on whether they were from a predator-naive or predator-sympatric population (Bell 2005; Dingemanse et al. 2007).

Despite well-documented differences in personality types, it should be noted that the underlying mechanisms responsible are seldom known. Personality type differences have been found to be explained by environmental factors, genetic differences or a combination of both among different populations (Sih et al. 2004).

South Island robins (*Petroica australis*) present an ideal study species for personality studies. They are known to be curious and tame in comparison to other avian species, and can be easily observed in the wild. This provides an opportunity to conduct experiments within the territories of free-living individuals. Robins also provide an opportunity for comparative studies, as populations exist both on the mainland (where they are sympatric with a wide variety of introduced mammalian predators) and on offshore islands (free of mammalian predators). If exposure to a high risk of predation selects for changes in personality one would expect individuals in mammalian-free areas to be bolder on average than birds on the mainland. In this chapter, I compared the boldness of robins in two populations that differed in exposure to mammalian predators by timing an individual's willingness to approach a human researcher in order to collect an item of food. Shyness and hesitation may lead to missing foraging opportunities or losing higher quality territories, and the resulting less fit birds and their offspring may be less likely to pass on their genes or survive. Alternatively, on the mainland, predation is the greatest cause of mortality (Brown 1997; Armstrong et al. 2006; Boulton, Richard & Armstrong 2008) and birds are less likely to face density-dependent mortality. Being shyer should mostly be advantageous, as birds will hesitate and scrutinise foraging opportunities and be more likely to fear and avoid novel objects and thus avoid predation.

METHODOLOGY

STUDY SITES

This study was conducted at two sites, one on the mainland of New Zealand near the town of Kaikoura, and one on a predator-free offshore island in the Marlborough Sounds. Kaikoura is located on the South Island. Robins were studied in two forest patches in this area, one at Kowhai Bush (-42.376,173.616) and another at Waimangarara Bush (-42.341,173.659). Kowhai Bush is approximately 240 ha in area and is dominated by kanuka (*Kunzea ericoides)*. The understory is composed of various native and introduced shrubs. For a more detailed description, see Hunt (1979).

Waimangarara Bush is approximately 65 ha in area and located approximately 5 km to the north of Kowhai Bush. It is composed of similar vegetation and holds a similar diversity of bird species. The two sites are joined through a continuous band of montane forest at their western edges but are otherwise separated by farmland. Kowhai Bush receives little predator control, and this primarily targets possums via baits and traps around the perimeter. Waimangarara Bush had been subject to more extensive predator control prior to this study, however, pest control efforts were similar to that of Kowhai Bush during this study (Barry Dunnet, *pers. comm.*). There was no significant difference between Kowhai Bush and Waimangarara Bush ($p > 0.05$), in the analysis so these were combined into one location. Introduced mammalian predators that are present at the Kaikoura sites include feral cats (*Felis catus*), stoats, (*Mustela erminea*), ferrets (*Mustela putorius furo*), weasels, (*Mustela nivalis*), rats (*Rattus rattus* and *Rattus norvegicus*), mice (*Mus musculus*) and possums (*Trichosurus vulpecula*).

Motuara Island is a 59 ha offshore island located in the Marlborough Sounds (-41.093,174.271). Forest structure is similar to that at Kaikoura (Maloney & McLean 1995).

The island has been mammalian-predator free since 1990 when Polynesian rats (*Rattus exulans*) were eradicated (Maloney & McLean 1995). Robins were introduced in 1973 from nearby Nukuwaiata Island (Taylor, Jamieson & Armstrong 2005). In contrast to the wide range of introduced mammalian predators present on the mainland study site, neither the source population on Nukuwaiata, nor the current descendent population on Moturara Island has ever been exposed to any mammalian predators other than Polynesian rats for any of their evolutionary history, though even this predator is no longer present (Maloney & McLean 1995).

STUDY SPECIES

SOUTH ISLAND ROBIN *PETROICA AUSTRALIS* (TOUTOUWAI)

South Island robins (hereafter referred to as robins) are an endemic passerine forest bird. They are insectivorous and largely feed on the ground. Breeding pairs are territorial and the male feeds the nesting female while both parents feed their nestlings and fledglings. Excess food items are cached for later consumption. Breeding occurs between September and January and 2-3 clutches are produced per season (Powesland 1983). Robins are well known for appearing to be fearless and inquisitive around humans. Most of the adult birds at both Kaikoura and Motuara Island had prior experience with researchers and many had already been fitted with unique colour band combinations so that individuals could be identified. Robins at both sites have been visited by researchers at similar levels and it is unlikely that one population was more habituated to receiving food rewards than the other. Alternatively, if trapping for banding had made them more fearful of humans, this has also been consistent between the populations. Robins evolved without the presence of any mammalian predators until introduced by humans but co-evolved with avian predators such as falcons (*Falco novaeseelandiae*) and owls (*Ninox novaeseelandiae* & *Sceloglaux albifacies*).

MEASUREMENT OF PERSONALITY

The relative boldness of robins was determined by their willingness and time taken to approach a human researcher. As the robins at both sites have experience with humans, the situation was not novel (*i.e.*, all had seen humans previously) but could be still be judged as a risky. Researchers walked around the study sites both on and off marked trails. Robins were attracted by making noise, including stomping, clapping, whistling and calling. When a bird appeared, it was fed a single mealworm (*Tenebrio molitor* larvae) to keep its interest during the experimental setup. This consisted of clearing the leaf litter from three patches of ground in a straight line. The patches were 30 cm, 100 cm and 300 cm from where the researcher stood motionless. When the robin was within five metres of and facing towards the researcher, five mealworms were placed at one of the patches and the approach time (latency) and total time to remove all five mealworms by the robin were noted. Once all five mealworms were consumed or removed, the researcher waited 1 minute before placing another 5 mealworms in a second patch. Once the second 5 mealworms were removed, the test was repeated a third time in the last remaining patch. The order in which each patch was tested was chosen randomly. If a robin failed to approach a patch within 5 minutes (*i.e.,* it was present but too shy to approach the patch), the worms were collected and the total time noted as 300 seconds. Latency was defined as the time (in seconds) taken to remove the first mealworm. Total time (in seconds) was defined at the period taken to remove all five mealworms. Handling time was defined as the difference between latency and total time. Only adult birds were used and only when they were able to complete the trials unhindered by other birds. If a neighbouring robin disrupted the trial, the researcher reattempted the test further from the presumed territory border. If the robin had a mate or fledglings present, the trial was only carried out if the other birds did not take worms directly, although they were often fed by or begged at the participant bird. The banding records were later checked to

confirm the sex of each bird. Where possible, birds were retested up to 3 times with a period of at least 24 hours between tests in order to be able to obtain a repeatability estimate.

STATISTICAL ANALYSIS

A binomial general linear model was used to compare whether or not a bird approached the mealworms for each distance. Linear models were used to compare the times taken to approach and remove mealworms at each location and distance. All times were transformed using natural log as they were not normally distributed. For this analysis, only the first test of each individual was used, to avoid pseudo-replication.

Repeatability was calculated with using the variance components of individual bird and trial number, using ANOVAs following the methods described in Nakagawa and Schielzeth (2010), Reale et al. (2007) and Lessells and Boag (1987) to see if latency at each distance was repeatable within individuals. It was calculated using the individuals that were tested in three trials.

A critical value of 0.05 was used in all tests. Statistical analyses were performed using the program RStudio, version 0.98.501.

RESULTS

Eight birds (4 male, 4 female) were tested in Kowhai Bush and 21 birds (16 male, 4 female, 1 sex unknown) in Waimangarara Bush, for a total of 29 birds tested in the mainland sites at Kaikoura (20 male, 8 female, 1 unknown). Eighty-five birds were tested on Motuara Island (56 male, 26 female, 3 sex unknown).

PROBABILITY OF APPROACH IN RELATION TO DISTANCE

The robins on Motuara Island were more likely to approach the mealworms at the two nearest distances than robins at the mainland sites in Kaikoura (figure 1). There was a significant difference between the two locations at the closest distance of 30 cm ($p < 0.001$) and at 100 cm ($p = 0.006$) but not at the furthest distance of 300 cm ($p = 0.104$). There were no significant differences between sexes and this variable was excluded from the final model.

LATENCY, HANDLING AND TOTAL TIMES

Robins on Motuara Island were quicker to approach the mealworms than robins at Kaikoura (figure 2). There was a significant difference in the latency between robins at Kaikoura and on Motuara at 30 cm ($p < 0.001$), 100 cm ($p < 0.001$) and 300 cm ($p = 0.007$). There was no difference between sexes and this factor was removed from the final model. The latency time was found to be highly repeatable at 30 cm ($r=0.557$) and at 100 cm ($r=0.714$) but not at 300 cm ($r<0.00$).

Robins on Motuara Island were faster in their handling of the mealworms than robins at Kaikoura (figure 3). There was a significant difference in the handling time between robins at Kaikoura and on Motuara at 100 cm ($p<0.001$) and 300 cm ($p<0.001$). The handling time difference at 30 cm was marginally not significant ($p=0.092$). There was no difference between sexes so this factor was removed from the final model.

Robins on Motuara Island were faster in the total time taken for removal of all mealworms than robins at Kaikoura (figure 4). There was a significant difference in the total time between robins at Kaikoura and on Motuara at 30 cm ($p<0.001$), 100 cm ($p<0.001$) and 300 cm ($P<0.001$). There was no difference between sexes so this factor was removed from the final model.

DISCUSSION

Robins on Motuara Island were found to be bolder than robins at Kaikoura. This was shown by their increased willingness to approach closer and by a reduced latency time to approach a researcher to retrieve mealworms. Although robins may not necessarily view humans as predators, approaching a larger animal should still be considered risky, as suggested by the difference in approach distances and latency times I observed. This difference is likely due to differences in predation risk, as Motuara Island currently has no introduced mammalian predators, while for mainland robins, predation is the highest cause of mortality (Powesland 1983). On Motuara Island, robin densities are around ten times greater than on the mainland (Mackintosh & Briskie 2005) and it is possible that bolder individuals would be more successful competitors in gaining territories, mates and food. Alternatively, at the Kaikoura sites, where interspecific competition is less intense, shyer personalities may be more advantageous as they may make them better at avoiding mortality through predation from a wide range of introduced mammalian predators that are present.

If an anti-predator behaviour (*i.e.*, being shy) is costly, it should be lost or diminished in a population in the absence of predators (Blumstein 2002). Other studies have shown similar tradeoffs between foraging and shyness. For example, in fallow deer (*dama dama*) bolder females raise heavier calves but suffer from higher predation than shyer deer (Bergvall et al. 2011). The shyer females may be subject to less predation but their calves are more likely to be smaller or starve. In Trinidad killifish (*Rivulus hartii*), bolder individuals grew faster and dispersed further than shyer fish (Fraser et al. 2001). Bolder Namibian rock agamas (*Agama planiceps*) spent more time basking and feeding and had larger territories but were depredated more than their shyer counterparts (Carter, Goldizen & Heinsohn 2012a). If robins experience a similar tradeoff, it is likely that being bold would be selected for in

populations subject to low predation risk. Robins on other mammalian predator-free islands have also been noted, anecdotally, to be tamer and bolder than mainland robins.

Although these results are consistent with differences in predation risk explaining the differences observed in personality traits, there are alternative explanations that cannot be ruled out. For example, it is possible that my sample of birds included a biased number of bold individuals at either or both sites. This would be the case if the shyest birds were too timid to even approach the experimental setup. However, if this was the case, I would not necessarily expect to still see differences in how birds responded at the experimental setup if only the bold individuals approached. Also, assuming only the boldest birds of Kaikoura approached, I would expect to have less difference between the sites. Despite this, there was still a difference in the average boldness between the two sites

The differences in personality could also be due to differences in food availability between the two study sites, as population densities are higher on Motuara Island than the mainland (primarily because of the high number of introduced predators on the mainland). Risk taking is likely to be higher when an animal is in poor energetic state (Verdolin 2006; David et al. 2012). However, robins at both sites continued to cache food when they are not immediately hungry and were eager to collect food from a researcher. The birds that did not approach to collect mealworms were typically observed to hop back and forth looking directly at the mealworms, suggesting they were motivated to approach, but too shy to come any closer. It has also been found that food supplementation did not appear to have an effect on nest and fledgling survival on Motuara Island (Mackintosh & Briskie 2005), suggesting that food limitation (hunger level) was not the underlying factor for differences I observed.

From this study, it is not possible to determine whether differences in average bold-shyness are due to genetic or learned influences or a combination of both. Some personality studies

have found that personality is genetic (Drent, van Oers & van Noordwijk 2003; Dingemanse et al. 2004) and heritable (Bize, Diaz & Lindstrom 2012; Brent et al. 2014) but others show that environmental factors have a stronger influence while heritability is less important (Fox & Millam 2004; Groothuis & Carere 2005; Chervet et al. 2011; Nicolaus et al. 2012). The ability of robins to adapt to novel predators (as discussed in chapter 3) suggests they have a degree of plasticity in how they behave and that predator recognition may be experience dependent (Maloney & McLean 1995; McLean, Hölzer & Studholme 1999). Different species likely have differing levels of plasticity, on individual and evolutionary levels, and New Zealand species lacking this ability to adapt to novel mammalian predators have likely already become extinct. Some studies have shown that plasticity itself varies between different populations (Richardson 2001; Dingemanse et al. 2012), especially if the population experiences changes within lifetimes. It appears that individual robins can learn and plastically change their behaviour in response to altered predation risk (McLean et al. 1999), but that environment conditions can guide selection toward certain behavioural traits in general.

My results showed that robins appeared to be consistent in their latency time to approach the researcher at 30 cm and 100 cm but not at 300 cm. This could be because of the difference in riskiness between the distances. It is possible that at the two closer distances, the time taken to approach is dictated by the personality of the individual while at the furthest distance the risk is so low that no difference between individuals is apparent. The repeatability estimates were comparable to other studies, as reviewed in Bell, Hankison and Laskowski (2009) which suggests that an $r > 0.30$ is sufficient evidence for repeatability in relation to animal behaviour.

FUTURE STUDIES

There is potential to carry out a range of further studies relating to personality differences between island and mainland populations of birds. Robins are an ideal study species for personality work as they are tame towards humans and do not need to be forced into unnatural situations to be tested. This is a problem which plagues many other personality studies involving caged animals in a laboratory setting. Nevertheless, it should be possible to adapt many lab studies to wild robins to determine how robins compare in other personality measure scales other than the bold-shy continuum and if these other measures differ consistently between island and mainland populations. It would be of particular interest to find out if the personality differences have a genetic basis, as has been found in great tits (*Parus major*) (Drent et al. 2003; Dingemanse et al. 2004) and blue tits (*Cyanistes caeruleus*) (Kluen et al. 2012). This could be achieved via translocation experiments, to see whether or not bolder island birds or their offspring stay bold or become shyer when moved to the mainland or vice versa.

It would also be interesting to see if other bird species on the island have differing average personality traits on the bold-shy continuum to those on the mainland. For example, blackbirds (*Turdus merula*) on Motuara Island appeared tamer and spent more time on the ground and alarm called less than those at Kaikoura (*pers. obs*.). Although the exact methods used in this study would not be applicable, there are plenty of other tests used in other studies cited here that could be adapted to this species. For example, differences have been found between fostered rural and urban blackbirds, suggesting that their behaviour has a genetic basis (Miranda et al. 2013). Hence it is possible island blackbirds would display differences also.

CONSERVATION IMPLICATIONS

As discussed in chapter three, translocation from island or captive-bred populations is currently a popular method of sustaining or reintroducing mainland populations (Seddon, Armstrong & Maloney 2007). There may be problems with this method, unless mainland predator populations are heavily controlled. In addition to lacking predator recognition or appropriate responses, the bolder birds or their descendants may be more prone to predation when faced with the range of mammalian predators on the mainland. We are currently lacking information about the ability of robins to learn and retain knowledge about predators over time and multiple generations, and especially whether such ability is related to an individual's personality. Some studies have began to look at the possibility of training naïve robins to recognise predators (Maloney & McLean 1995; McLean et al. 1999; Whitwell et al. 2012) but not yet in relation to their personality types. Short-term training can be successful in some instances (*i.e*., the gain of predator recognition abilities) while another study showed that robins lost recognition of rats after one generation of isolation (Jamieson & Ludwig 2012). Both patterns suggest that predator recognition is less innate and more experience-dependent. Perhaps in robins, predator recognition may be regained more readily as they share congeners with continental species, suggesting less isolation from mammalian predators than species with longer evolutionary periods of isolation (Blumstein 2006; Seddon et al. 2007). Studies have shown that individuals in some species with certain personality traits learn faster and retain information better than others (Brown et al. 2013; Guenther et al. 2014). Given the differences I found in personality between island and mainland robin populations, it would therefore be worthwhile investigating how personality affects predator training in robins and other New Zealand birds destined for relocation. If "shy" personalities prove more able to recognise novel predators, and be trained to avoid them, this gives hope that future translocations can be tailored to also include environments with predators.

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FIGURES

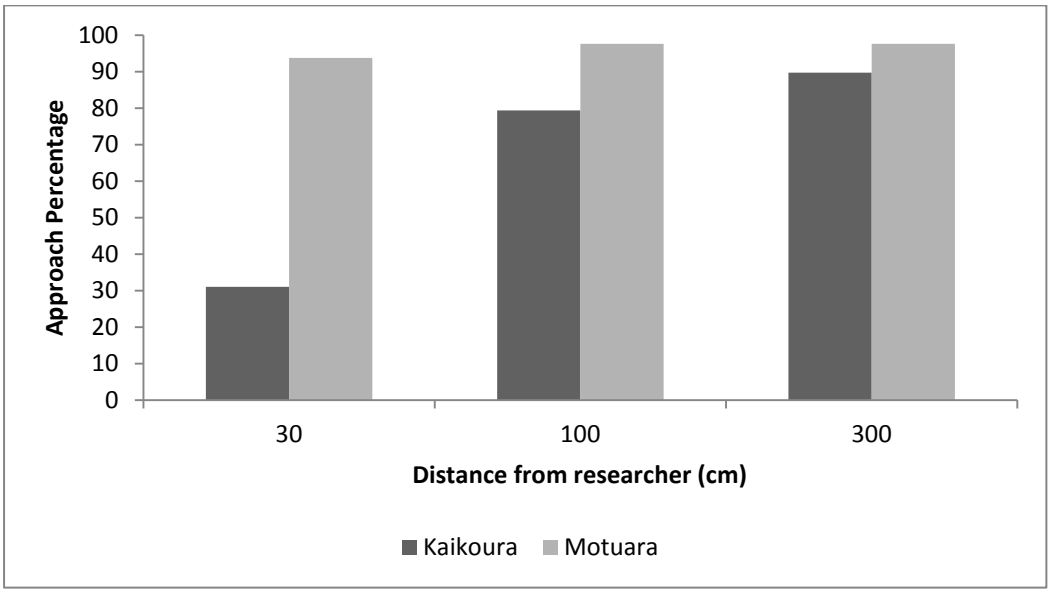

Figure 1: Percentage of South Island Robins at Kaikoura (mainland site) and on Motuara Island that approached a researcher to retrieve mealworms at 3 distances.

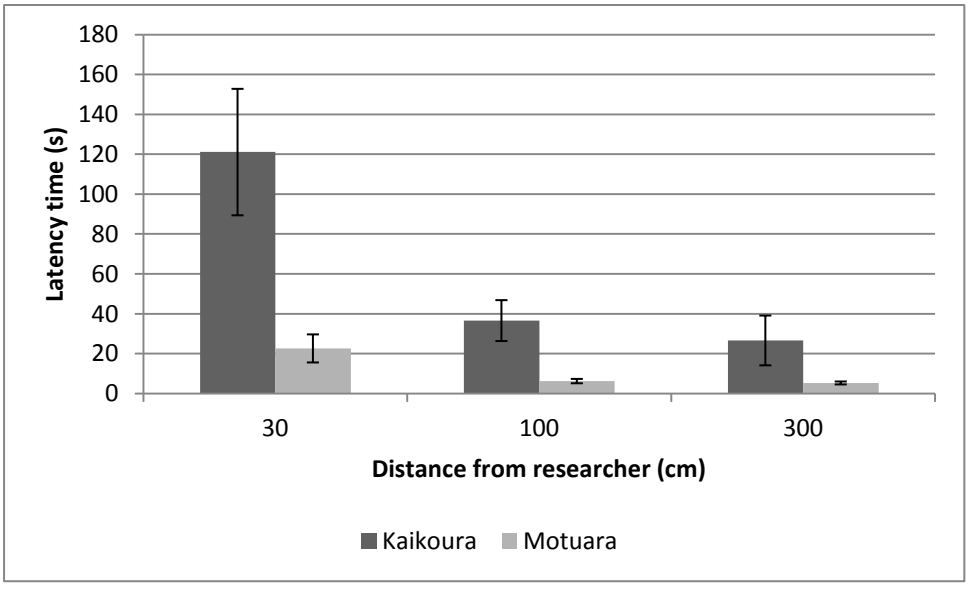

Figure 2: Mean latency times for South Island robins to approach and remove the first mealworm at 3 distances from researcher at Kaikoura (mainland site) and on Motuara Island. Note that data was non-Gaussian and transformed for statistical models. Figure is for presentation purposes only (see text for statistical analyses).

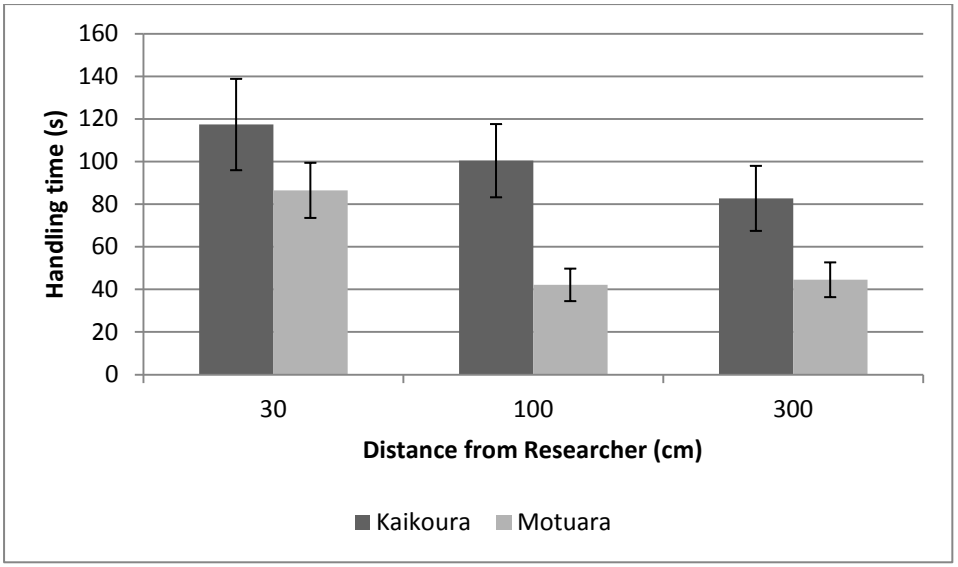

Figure 3: Mean handling time for South Island robins to remove 5 mealworms, from first to last mealworm, at 3 distances from researcher at Kaikoura (mainland site) and on Motuara Island. Note that data was non-Gaussian and transformed for statistical models. Figure is for presentation purposes only (see text for statistical analyses).

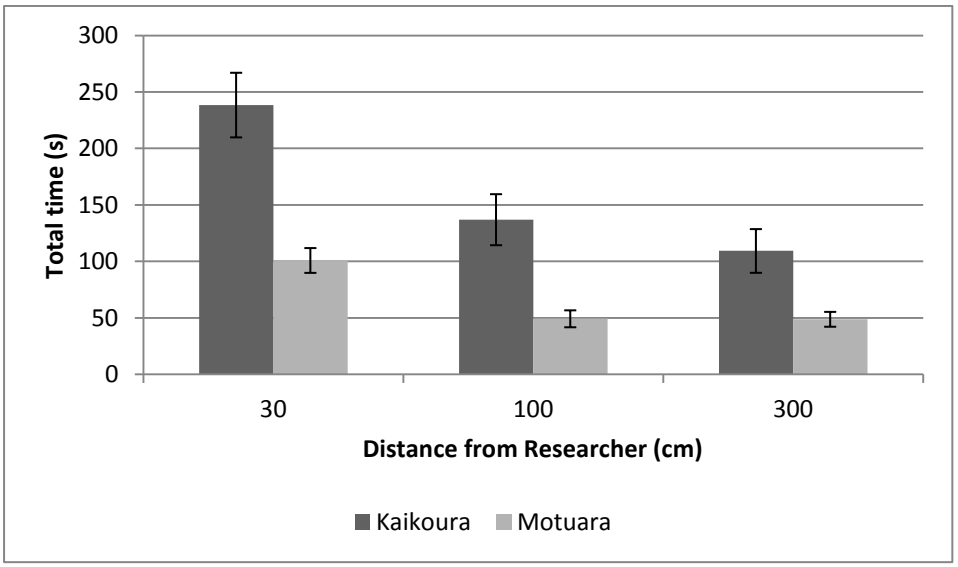

Figure 4: Mean total time for South Island robins to finish removing 5 mealworms at 3 distances from researcher at Kaikoura (mainland site) and on Motuara Island. Note that data was non-Gaussian and transformed for statistical models. Figure is for presentation purposes only (see text for statistical analyses).

CHAPTER FIVE: GENERAL DISCUSSION

My results have shown differences in predator recognition ability across a number of native and introduced New Zealand birds based on their evolutionary history and geographic isolation with different types of predators. In at least one species, I also found evidence for personality differences in the "bold-shy" behaviour. These differences are consistent with differences in predation risk experienced between the different species and populations. Predators can have a large influence on shaping the behaviour and life history traits in birds (Montgomerie & Weatherhead 1988), and in their absence, such anti-predatory traits may be altered, diminished or disappear altogether.

RESEARCH SUMMARY

In chapter two, I examined how New Zealand birds reacted to the presence of model predators at their nests. I aimed to determine if anti-predator responses had disappeared in the absence of one of the most important predators in continental avifaunas, namely snakes. My data suggested that New Zealand birds, both native and introduced, do not appear to have any recognition of snakes. In the case of native birds, they have never occurred sympatrically with snakes and thus it is not surprising they show no recognition or anti-predatory adaptations to them. In contrast, introduced birds appear to have lost any recognition they may have had from when they co-occurred with snakes in their native ranges. This could be due to the recognition trait being costly and thus lost (*i.e.*, a genetic change since their introduction to New Zealand) or due to individuals needing experience to be able to learn recognition (*i.e.*, a learnt recognition that has been lost in the absence of the stimulus).

I also aimed to determine if mainland native birds, which have been exposed to kiore (*Rattus exulans*) for *c.* 1000 years and a range of additional mammalian predators for *c.* 130 years

(King 1984) have adapted and are able to recognise them as a threat. Although I was unable to test the recognition abilities of native birds to all of the introduced mammalian predators, it does appear that they have developed the ability to recognise stoats (*Mustela erminea*), as all native species showed response levels that were similar to that of a morepork (*Ninox novaeseelandiae*), a historical and current predator. My results do not allow me to determine whether this recognition is genetic or learned, but given the relatively short time since native birds have been sympatric with stoats, it is possible that recognition has occurred by simply extending pre-existing anti-predatory responses, such as that given to native predators (*i.e.*, owls), to a non-native predator. Such a rapid change is consistent with the idea that animals can be phenotypically plastic and environmental factors or learning is important in behavioural trait development. Furthermore, some species such as starlings and rifleman appeared to react to any novel object near their nest. Such a general response to any intruder at the nest could give an advantage should any new predators succeed in invading New Zealand.

In chapter three, I examined the difference in response to model predators between two populations of South Island robins (*Petroica australis*) that varied in predation risk, with one population on the New Zealand mainland that is sympatric with a range of introduced (and native) predators, and a second population on an offshore island that is sympatric with native predators only. My data confirmed that robins on the mainland have the ability to either learn about or adapt to novel predators such as stoats. This is shown by the fact that mainland robins displayed a number of anti-predator responses toward taxidermic mounts of a stoat at their nest, at the same level as they did to a taxidermic mount of a morepork, whereas island robins responded only to the morepork and not the stoat. This difference could again be due to mainland robins having directly experienced stoats, such as close calls or seeing other

birds being attacked, or due to genetic differences that have developed with the introduction of stoats to mainland New Zealand.

Finally, in chapter four I investigated whether South Island robins displayed consistent personalities on the bold-shy continuum. I hypothesised that the two robin populations with differing predation risk would have different average levels of bold and shyness. My results suggest that robins on the mainland are less 'bold' on average than those on a predator-free island. The difference in personalities is likely due to the differing predation risk. Bold individuals tend to be more tame and curious and less risk aversive than shyer individuals (Sih, Bell & Johnson 2004). Selection processes may have acted against bold individuals on the mainland (due to increased risk of predation) and shy individuals on the island (due to tradeoffs with other behaviours such as foraging or via competitive pressures), resulting in the divergence of average personality traits. The difference also may depend on learning and experiences of each individual. It could also be phenotypically plastic, having a genetic basic but depending on experience to cement the personality.

MECHANISMS OF PREDATOR RECOGNITION

My results illustrate that there are a mixture of phylogenetic and ontogenetic factors and processes that may influence how animals behave towards predators.

Evolutionary processes are likely to be acting on whether or not an animal recognises a predator and how it responds (Martin 1995; Blumstein 2002; Dingemanse et al. 2009). Founder effects may have played a role in what traits persisted in the original populations when they first established in New Zealand, particularly since most species have experienced some degree of bottleneck with only minor gene flow (Worthy & Holdaway 2002). For example, it is thought that the native avifauna experienced bottlenecks, both when originally

colonising and as a result of changing shorelines of the New Zealand landmass over the last 80 million years (Cooper & Millener 1993), and more recently through anthropomorphic habitat changes (including the introduction of novel predators). The South Island robins on Motuara Island experienced a particularly severe bottleneck during translocation and are descended from five individuals (Mackintosh & Briskie 2005), although when I studied them they had been "rescued" through the introduction of birds from another population (Heber et al. 2012). Introduced species were also established via low numbers of founding populations (Thomson 2011). Thus, many species likely have lost genetic diversity, and this may have included the loss of alleles associated with predator recognition. Other stochastic processes such as drift may have similarly led to traits being lost.

Apart from founder effects or drift, selection pressure from predation is expected to lead to changes in genotypes associated with predator recognition. Predators are known to induce high selection pressures and have led to changes in behaviour (Réale & Festa-Bianchet 2003). Conversely, relaxed selection has been shown to result in behavioural traits being lost, especially if they are costly or have trade-offs with other activities such as foraging or parental care (Blumstein & Daniel 2005). Nevertheless, the loss of predator recognition can potentially be reversed when a population comes into contact again with a previously allopatric predator guild. Such a process may explain the ability of native New Zealand birds to recognise novel predators. Prior to the introduction of mammalian predators, New Zealand birds did have ability to avoid predation by avian predators. This ability may have plastic enough to be used for protection against predatory mammals as well as predatory birds. Although the mechanisms of predator recognition in the New Zealand birds I studied are unknown, studies of other species indicate genetic processes are likely to have had a role. For example, naïve individuals in some species (*e.g*. in hatchlings of domestic fowl (*Gallus gallus domesticus*), Seychelles warbler (*Acrocephalus sechellensis*) and Australian brush-

turkey (*Alectura lathami*)) have been shown to be able to recognise and respond appropriately (Veen et al. 2000; Göth 2001; Zidar & Løvlie 2012). It is likely that genetic traits are the basis of predator recognition ability in these and other species (Bize, Diaz & Lindstrom 2012).

The ability to recognise and respond appropriately to predators can vary among individuals and populations of the same species, so it is also highly likely that experience plays a role in how individuals react. Experiencing a "near miss" or cultural transmission via witnessing other birds react towards a predator (Curio, Ernst & Vieth 1978) may aid in development of predator recognition. Alternatively, some species have been shown to have lost predator recognition in as little as one generation after being translocated to a predator-free island (Jamieson & Ludwig 2012). Their lack of recognition may be due to lack of opportunities for learning and experience with a predator. For example, young birds may be able to learn the identity of predators by observing their parents or other conspecifics (*e.g*. alarm calling to a predator). In the absence of a predator, such learning cannot occur and will be culturally lost. Therefore, it is possible that some of the birds in my study required a learning event or experience to recognise my models as a threat, explaining some of the variation I observed. Individuals can also be phenotypically plastic and may be flexible in their behaviour in accordance to risk in the environment (Fontaine & Martin 2006; Lima 2009).

As our understanding of epigenetic mechanisms increases, it has become apparent that the state of an individual may affect the genes of their offspring (Storm & Lima 2010; Stratmann & Taborsky 2014). Changes in predation risk may cause stress upon an individual which may alter how their offspring develop and display certain traits (Sheriff, Krebs & Boonstra 2010; Stratmann & Taborsky 2014). This may include anti-predator behaviours and personality traits, although further research is needed to explore to what extent this mechanism operates.

If epigenetic processes are a factor, it may aid species in quickly adapting to changes and possibly have resulted in the lost or gained predator recognition demonstrated in my research.

The above factors and processes are not mutually exclusive and a combination is likely to be acting on each species, population or even individual to influence how predator recognition and avoidance is exhibited. As demonstrated in chapter four, individual animals have been shown to have personalities which result in consistent behavioural variation (Sih et al. 2004). Robins on mammalian predator-free Motuara Island tended to be bolder than those on the mainland near Kaikoura. Personality may have also played an important role in the results of chapters two and three. There was a wide variation in response to predators, suggesting that individual personality may be influencing how each bird behaved. It would be interesting to repeat the model presentations on the same individuals (such as riflemen or robins, which can be identified via their unique colour bands) to see if nest defence behaviour was repeatable, as has been found in other studies (Hollander et al. 2008) or correlated with other personality trait scales (Herde & Eccard 2013).

By exploring which influences are dominant, it can help us understand how life history traits develop. Such information adds to our understanding of the factors which cause island species to become vulnerable to exotic invasions. It also has practical applications, such as in evaluating potential for translocation and restoration efforts.

CONSERVATION IMPLICATIONS AND FUTURE RESEARCH

Predator recognition abilities are an important part of avoiding predation. Predator naive populations are particularly vulnerable to the introduction of introduced predators, as recognition may be lost or forgotten or need to be learned first (Blumstein 2006). This places the New Zealand avifauna at risk if any new species such as snakes manages to establish

here. It also shows that birds on island sanctuaries are vulnerable when mammalian predators do reach the shores, as has been shown to happen occasionally (King et al. 2014). Hence, biosecurity efforts on a national and local basis are crucial for continued protection.

Translocation is a popular tool for restoring degraded habitats via reintroduction of locally extinct fauna (Seddon, Armstrong & Maloney 2007). However, if predator naive or bold populations are used as a source, there is a risk that these individuals will be particularly vulnerable to predation. This shows the need to continue efforts to control and eradicate predators on the mainland, while also attempting to train any animals translocated from islands (Van Heezik, Seddon & Maloney 1999; Griffin, Blumstein & Evans 2000; Azevedo & Young 2006). Studying how translocated birds behave towards predators will help improve reintroduction science and choosing suitable source populations.

This research has shown the differences between different populations and species in their predator recognition abilities. There are multiple opportunities for future research to explore the exact mechanisms that cause the difference. For example, the tests performed here could be repeated over several years and generations to see whether the nest defence behaviour and personality traits are consistent among individuals and heritable by offspring. Eggs could be cross fostered between the island and mainland to see whether offspring display their inherited parents' traits or adaptive traits suited to their current environment. As it seems unlikely that predatory mammals will be eradicated from the main islands of North Zealand in the near future (or ever), the best opportunity we have to ensure that native birds survive in areas outside intensively managed reserves is to somehow encourage them to become "street-wise" and acquire the adaptations they need to co-exist with the novel predators they now face. My study confirms this is not an unrealistic possibility. The next step is to determine the mechanisms by which such adaptations have been acquired and whether there is something we can do to facilitate this process.

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